Deer, biodiversity management and ecotourism in the Hebrides: conflict or mutual benefit

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ABSTRACT

A new management scheme is planned for an island estate in the Inner Hebrides, and aims to promote short-sward biodiverse grassland habitats through controlled grazing pressures and distribution of red deer, whilst avoiding the negative impacts of deer overabundance. These habitats are biodiverse, and act as important refugia for Zygaenidae, a group of day-flying moths with strongly restricted distributions elsewhere in the UK. Traditionally, sheep grazing is used in the region to maintain grasslands, however, this results in an intensively grazed grassland that is not suitable for Zygaenid moths. Red deer may create preferable habitat conditions for the moth species, as human-linked disturbance will cause the deer to balance foraging with anti-predatory behaviours. Whilst the nature and impacts of red deer grazing upon various vegetation communities has been thoroughly investigated, the applicability of red deer as a viable conservation grazer has not been studied. Furthermore, the impacts of human presence upon ecosystems via the alteration of the behaviour and patterns of habitat use of a key grazer have not been linked in disturbance ecology.

Therefore, the main aim of this thesis was to examine the behavioural and habitat use patterns of red deer in response to human-linked disturbances that vary spatially and temporally. Utilizing the red deer as a primary grazing species, it was imperative to understand the impacts that increasing levels of tourism may have had on the behaviour and consequently grazing intensity and habitat use of the red deer. In appropriating the path systems on the island as an index for human-linked disturbance, key red deer behaviours and patterns in habitat use were mapped temporally (diurnal and seasonal) in relation to the proximity, traffic and visibility of path systems, at both fine and coarse scales. Consequently, the impacts of tourist activities on red deer throughout the south-side of the island were quantified. Additionally, these impacts were linked to the abundance of a day-flying moth, *Zygaena purpuralis*, which acted as a bioindicator for the short-sward grasslands. Moreover, the vegetative requirements of the moth were identified at varying spatial scales.

In areas of frequent and high human activity, deer exhibited a reduction in anti-predator behaviours by occupying areas associated with human presence. However, in areas with relatively low amounts of human activity, deer routinely disrupted foraging bouts by engaging in anti-predatory behaviours and avoided areas close to paths. These latter patterns were exhibited in the short-sward grassland areas. *Z. purpuralis* abundances were higher in areas of high deer presence, and both deer and *Z. purpuralis* favoured areas with high vegetation diversity. Additionally, *Z. purpuralis* abundances were higher in areas that featured deer trails, and bracken had a strong negative influence on abundance at a variety of spatial scales.

By controlling these patterns of habitat use and foraging behaviours of a wild ungulate, human presence can indirectly dictate the grazing regime experienced in certain habitats. In the case of the island estate, the population of *Z. purpuralis* in the grassland habitats benefited from the behavioural patterns of deer adopted in response to the levels of tourist activity in the area. Additionally, red deer provided bare soil, an important habitat requirement of *Z. purpuralis* through the creation of deer trails. Aside from proving that red deer are a viable grazing tool for land management schemes, this thesis has also provided the first evidence of human activity impacting upon the ecological landscape by altering the behaviour and patterns in a grazer through disturbance.

DECLARATION

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Hagen Metzing O'Neill

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CHAPTER 1

GENERAL INTRODUCTION

‘Sweet is the lore which nature brings,

Our meddling intellect

Mis-shapes the beauteous form of things: -

We murder to dissect’

- William Wordsworth

1.1. OPENING STATEMENT

A new management scheme is planned for an estate in Scotland, whereby red deer (*Cervus elaphus*) are used as conservation grazers for biodiverse short-sward grasslands. Since the deer on the estate are wild ungulates, the behaviour of these animals is likely affected by tourist-related disturbance. As such, the purpose of this thesis is to study the impacts of tourist activity upon the behaviour and habitat use of red deer and investigate the potential ecological consequences of the behavioural shifts. The indirect ecological impacts of human-linked disturbance have not been previously researched, and so this thesis represents the first study of these cascading effects. The underlying rationale for this aim is described in the current chapter. First, ecotourism is introduced, and the recent growth of this industry is detailed. Then, the impacts of human-induced disturbance upon wildlife are discussed. In using red deer as a conservation grazer in Scotland, it is important to note upon the unique situation of deer and land management in Scotland. As such, the history and biology of Scottish red deer are briefly summarised. Finally, the specific objectives of the land management scheme on the island estate are described, and the research questions of this thesis are detailed.

1.2. INTRODUCTION TO ECOTOURISM

Ecotourism, or wildlife tourism, has always been a stable element of tourism activities, yet recent years have experienced a rapid growth in this sector (MacLellan, 1999). This can be attributed to an increasingly partisan attitude of the public with regards to conservation efforts, the loss of biodiversity, environmental issues and habitats degradation (Gössling, 1999).

The underlying problem to most environmental/conservational issues stems from, or is related to human over-population. The total human population has increased from approximately just over a billion in 1900 to over 7 billion today (Cohen, 2003). Additionally, the obvious increase in resources demanded by such population growth, the *per capita* consumption of world products has increased by approximately 20 times (Daily, 2003, Holdren and Ehrlich, 1974). This presents a problem in using the Earth's resources sustainably, which can be exemplified by the following: the global annual net primary production (NPP) of photosynthetic products amounts to 225 billion metric ton, almost 40% of which are consumed directly/indirectly or wasted by human activities (Chapin III *et al*., 2011, Vitousek *et al*., 1986). This

brings a substantial loss in habitat due to human encroachment and infrastructure development, with subsequent declines in biodiversity (Worm *et al*., 2006). The importance of biodiversity is two-fold: the diversity and richness of species or phenotypes underlie the efficacy and extent of ecological processes and general ecosystem quality (Huston, 1997); secondly, in terms of economic benefits, biodiversity governs the provision of resources and services for human consumptive needs (Balmford *et al*., 2002, Pimentel *et al*., 1997). There is a growing public awareness of the implications of biodiversity loss, as there is a growing appreciation for the intrinsic value of biodiversity, and this is becoming ever more expressed through governments and mass media (McNeely, 1992).

One of the ways this concern over biodiversity loss has manifested itself is the recent development and interest in nature-based tourism, or ecotourism. For many industrialized countries, there is an increasing demand for nature-based activities, and as such public perception is placing great value upon protected areas (Gössling, 1999, Kiss, 2004). Ecotourism and wildlife-watching are becoming increasingly popular sectors of the tourism industry (Duchesne *et al*., 2000, Tadesse and Kotler, 2012), and with this any issues of growing disturbance to wildlife needs to be evaluated. Catering for this type of tourism involves modifying previously remote habitats and increasing the levels of contact between wildlife and humans through improved transport systems, and there are concerns for the impacts this trend may have on animal welfare, productivity and behaviour (Sibbald et al., 2011a). Alongside hunting, recreational activities is one of the two main causes of disturbance to wildlife species (Hamr, 1988, Nellemann et al., 2000b). However, as access to the countryside is increasing in the UK, the associated effects of disturbing wildlife are likely to increase (Beale and Monaghan, 2004b, Stankowich, 2008). Fully ascertaining and understanding the true impacts that human disturbance has on wildlife will allow public land managers to balance visitor access and species protection appropriately (Papouchis et al., 2001, Beale and Monaghan, 2004b).

Ecotourism can benefit conservation agendas through stimulating public interest in biodiversity and conservation projects, and in doing so provide financial assistance to such conservation work (Duchesne *et al*., 2000, Kiss, 2004). However, the practice of ecotourism should not put the future of the wildlife involved in jeopardy. Ecotourism is truly successful when its goals are harmonious with those of conservation management, but also by providing financial and educational contributions towards the biodiversity conservation at hand.

1.3. EFFECTS OF HUMAN-LINKED DISTURBANCE ON WILDLIFE

Predation is recognised as a major selective force, driving the morphological and behavioural characteristics of animals in evolutionary time, but it also influences behavioural decisions made by animals in ecological time (Lima and Dill, 1990). Behavioural adjustments are made by animals to balance the risk of predation with engaging in beneficial activities such as mating displays, parental feeding and foraging, and by selecting habitat that minimises predation risk (Lima and Dill, 1990, Anholt and Werner, 1995). The 'risk-disturbance' hypothesis (coined by Frid & Dill, 2002), states that human presence elicits similar responses in wildlife, and human presence is therefore analogous to that of a true predatory threat.

In support of this hypothesis, there are a range of studies revealing that disturbance effects are comparable to true predatory threats (Cassirer et al., 1992, Frid and Dill, 2002, Gander and Ingold, 1997, Jayakody et al., 2008, Manor and Saltz, 2003, Nellemann et al., 2000b, Papouchis et al., 2001), and numerous studies have proven negative impacts of tourists upon several species of wildlife (Duchesne *et al*., 2000). In general, disturbance stimuli forces wildlife to trade fitness enhancing activities in favour of numerous avoidance mechanisms (Duchesne *et al*., 2000, Fernández-Juricic and Schroeder, 2003, Tadesse and Kotler, 2012). Specifically, the effects of disturbance on wildlife are generally evaluated through measurements of behaviour, for example: foraging; vigilance; and resting behaviours have all found to be affected by human presence (Andersen *et al*., 1996, Fernández-Juricic and Schroeder, 2003, Fortin and Andruskiw, 2003, Freddy *et al*., 1986, Frid, 2003, Gander and Ingold, 1997). Furthermore, responses are realised in both short and long-term scales (Stankowich, 2008). Short-term behavioural responses include: a willingness to vacate suitable habitat, especially if the human disturbance occurs in a consistent or predictable pattern (Papouchis *et al*., 2001); the tendency to engage in flight behaviour (Bonenfant and Kramer, 1996); a reduction in parental care (Verhulst *et al*., 2001); and time spent foraging (Ronconi and Clair, 2002). These effects can be particularly deleterious as disturbance can trigger vigilance behaviours and/or flight responses, incurring energetic losses to such an extent that the survival and reproductive success of individuals is reduced (Papouchis *et al*., 2001). Long-term behavioural responses include: habituation to human presence (McLellan, 1990); altered activity patterns (Stockwell *et al*., 1991); and habitat use patterns (Thiel *et al*., 2008). Consistent disturbance has been shown to impact negatively upon species' biology, such as reproduction and physiology (Stankowich, 2008). Indeed, the risk-disturbance

hypothesis predicts that populations that are subject to sufficiently long-term and/or intense disturbance stimuli will decline due to a reduction in body condition and subsequent reduction in reproductive success (Frid, 2003, Frid and Dill, 2002). This is supported in the field by Hicks and Elder (1979), who suggest that in the case of several populations of bighorn sheep in the Sierra Nevada region, constant human disturbance is the single most important factor limiting population growth.

Red deer can be disturbed easily by tourists on foot (Cassirer *et al*., 1992), and Jayakody *et al.* (2008) found the species to make a clear trade-off in favour of vigilance behaviour over feeding time in habitats frequented more regularly by tourists in comparison to those in less disturbed habitats (Jayakody *et al*., 2008). In the American form of the species, human disturbance has been found to be associated with reduced calving rates in wapiti *C. elaphus canadensis* (Sibbald et al., 2011a). Tourists accompanied by dogs have shown to increase the extent to which deer aggregate and perform vigilance behaviours (Jayakody *et al*., 2011). *Canis lupis* once existed alongside *C. elaphus canadensis*, and dogs may trigger a ghost effect of species-specific anti-predatory behaviour. Duchesne *et al*. (2000) assessed the impacts of ecotourist visits on a herd of *Rangifer tarandus*, finding ecotourists to significantly reduce *R. tarandus* foraging and resting/ruminating time, primarily by increasing the standing-vigilance behaviour. The extent of time spent vigilant was positively correlated with the number of tourists observing the animals. When considering the potential impact of ecotourism-related disturbance on wildlife, it is important to appreciate that temporal differences in tourist activities can have severe effects on a species' well-being (Duchesne *et al*., 2000). For example, Scottish red deer are more commonly disturbed whilst in their feeding grounds during spring and summer when tourist activities increase (Jayakody *et al*., 2011). In Yellowstone National Park, the winter months feature an increase in skier disturbance which can significantly reduce red deer survival by increasing energy expenditure during this critical season (Cassirer *et al*., 1992).

In ungulates and other herbivores, anti-predatory behaviours are manifest in group sociality and herding strategies, and human disturbance has been shown to elicit a range of typical anti-predatory responses, such as the formation of larger groups and an increase in scanning behaviour (Fernández-Juricic and Schroeder, 2003, Jayakody *et al*., 2008). One of the more prominent advantages to sociality in herbivores is the early detection of predatory threats, through the combined vigilance of individuals in the group, i.e. the 'group size effect', in which individuals in a group can devote more time to feeding as the group size increases (Lima and Bednekoff, 1999). However, this view that individuals in a group pay

attention to the level of vigilance amongst conspecifics is not taken as a rule throughout the literature, and certain studies support the opposite (Cassirer *et al*., 1992, Duchesne *et al*., 2000, Fernández-Juricic and Schroeder, 2003). Group living may not provide an advantage of increased foraging time through shared vigilance for some species, but rather individuals benefit from the dilution of risk (Fernández-Juricic and Schroeder, 2003).

Whilst the documentation of human disturbance incurring risk-avoidance in wildlife is extensive, certain animals can exhibit habituation to prolonged or repeated human disturbance, and the impacts of ecotourists have been shown to decrease through repeated exposures (Duchesne *et al*., 2000). Red deer show habituation to predictable ecotourism, although seemingly habituated red deer can still exhibit strong aversion to human presence in unusual areas (Cassirer *et al*., 1992). Papouchis *et al*. (2001) found that bighorn sheep *Ovis canadensis* displayed greater flight responses to hikers than to road traffic, which could be due to the unpredictable tendency of hikers to approach sheep from a variety of locations. Furthermore, an increase in road users such as mountain bikers did not correlate with an increase in flight responses, suggesting that the sheep habituate to disturbance confined to designated paths regardless of traffic. Indeed, the eventuality that a given species may habituate to hikers is more likely with predictable path use, as opposed to unpredictable off-trail use (Hicks and Elder, 1979).

Such findings of habituation to human presence are incongruent with the 'risk-disturbance' hypothesis. In support of this, Duchesne *et al*. (2000) found that wolf presence elicited a significantly greater displacement effect on a *R. tarandus* herd in comparison to human presence, which seemed to cause no displacement whatsoever (Duchesne *et al*., 2000). Predatory disturbance causes animals to make a trade-off between net energy intake and mortality risk by adjusting their habitat selection choices and behaviour (Jayakody *et al*., 2008). As discussed, these choices and behaviours are elicited on occasion by wildlife in response to human presence. However, that wildlife can become habituated to human presence suggests the risk-disturbance hypothesis is a temporary phenomenon, losing effect through prolonged exposure.

1.4. A BRIEF DESCRIPTION OF SCOTTISH RED DEER BIOLOGY

Red deer are a relatively large species of cervid that exists within the 30-65° N latitude zone, with a disjoint Holarctic distribution (Clutton-Brock *et al*., 1982, Gössling, 1999). However, there is much

discrepancy amongst taxonomists on whether the different populations should be considered as forms of a *Cervus elaphus* complex, or that Eurasian and American populations represent two different species altogether (Ludt *et al*., 2004, Polziehn and Strobeck, 1998). The differences between Eurasian and American forms are certainly marked, notably in the size, colouring and vocalisations (Clutton-Brock *et al*., 1982), but the two forms readily hybridize in the wild (Mitchell *et al*., 1977), and a *Cervus elaphus* complex is assumed in most general accounts (Clutton-Brock *et al*., 1982).

Red deer exhibit strong sexual dimorphism, with adult stags weighing on average 25-30% more than hind counterparts (Catchpole *et al*., 2004). Like the majority of cervids, only stags grow antlers, characterized by an annual cycle of tremendous growth to maturation in the late summer, and cast the following spring (Price *et al*., 2004). The maximum lifespan is approximately 20 years. The species breeds seasonally with single births (Mitchell *et al*., 1976). In Scotland, the breeding season (known as the 'rut') begins in early autumn and ends in mid-November, with mating activity peaking in October (Clutton-Brock *et al*., 1979, Clutton-Brock *et al*., 1982, Lincoln *et al*., 1972). Pregnancy encompasses the winter and spring months, and calving begins in late May to late June (Mitchell *et al*., 1976). Lactation in hinds is relatively prolonged for ungulate species, and can persist until the following calving season (Mitchell *et al*., 1977). However, timing will vary with environmental conditions, and harsh winters may contribute to the delay or inhibit oestrus (Lincoln *et al*., 1972). Typical of ruminants, red deer form sexually segregated herds throughout most of the year (calves remain with hinds), coming together during the rutting period (Clutton-Brock *et al*., 1982).

As human activities have drastically altered the distribution and abundance of Scottish red deer, habitat selection is relatively unique for the species, with preference for open moorland and unwooded terrain, whilst continental populations rely on woodland as an important habitat as it provides woody browse and shelter (Mitchell *et al*., 1977). It is possible that the altitudinal variation of the Scottish countryside provides shelter, and the abundance of heather replaces tree browse. Indeed, deer do not seem to occupy flat unwooded terrain in Scotland, suggesting that the shelter provided by hilly country is an important prerequisite for occupancy (Clutton-Brock *et al*., 1982). Another common feature of Scottish populations is a diurnal altitudinal migration from higher altitudes to lower altitudes at dusk (Mitchell *et al*., 1977). It is reasoned that heather is browsed during the day, and grasses, sedges and forbs occurring at lower altitudes are grazed at night (Darling, 2008).

1.5. A HISTORICAL ACCOUNT OF RED DEER AND MAN IN SCOTLAND

The earliest records of red deer in Scotland are dated from the Late Pleistocene (Clutton-Brock *et al*., 1982). At this time, deer would have inhabited a very different environment than that of today, as over half of Scotland was covered in large swathes of birch, willow, alder and Scots pine (Lowe, 1961). Large tracts of open grasslands and heathlands similar to those of the Highlands would still have existed, and it is likely that deer would have performed both grazing and browsing feeding patterns (Clutton-Brock *et al*., 1982). Indeed, whilst most contemporary Scottish red deer populations are principal grazers, anatomical evidence suggests that red deer are adapted for a diet of mixed browse and graze (Hofmann, 1989). However, the quality of available forage in Scotland was poor, and this is generally assumed to be linked to the small body and antler size of Scottish deer in comparison to European forms (Huxley, 1931, Hyvärinen *et al*., 1977).

Humans most likely colonized Scotland between c. 12,000-10,000 BC by arriving on the west coast from Ireland (Mellars, 2004), and the earliest settlement in the Inner Hebrides is dated at c. 8500 BC (Edwards and Mithen, 1995). These settlements were mostly fishing-based, but infrequent deer hunting also occurred during this period (Finlayson, 1999). As such, these fishing-based societies had little impact upon the environment. Changes in land-use and the environment were first brought about by the arrival of Bronze Age peoples in eastern Scotland (c. 2500 BC) , who brought with them advanced agricultural practices, and cleared substantial deciduous woodland in favour of tillage and grazing land for livestock (Lowe, 1961).

Human impacts upon the Scottish landscape became progressively more ambitious from the Iron Age onwards: not only was more land required for a growing population, but timber was under increasing demand for construction and smelting activities (Finlayson, 1999). Simultaneously, the climate was warming and becoming more humid, which promoted the encroachment of bog at the expense of woodland in the upland areas (Steven, 1951). As such, it is estimated that almost 33% of Scottish woodland was lost to changes in the climate and anthropogenic activity (Lowe, 1961).

By the mid-15th Century, continued timber extraction and land conversion resulted in a landscape more modern in appearance, with little woodland existing outside of the Highlands area (Hobbs, 2009).

During this period Scottish red deer populations crashed to critically low levels as a result of two popular forms of land use in the region: hunting grounds and sheep farming. Firstly, large tracts of land were reserved by nobility as private hunting grounds, and unlike more modern British hunting culture, hunting was also practised by the common man (Lowe, 1961). Hunting was conducted at a large scale, and records indicate that over 100 individuals were taken regularly (Clutton-Brock *et al*., 1982). Secondly, sheep farming was the most profitable form of land use at this time, and was prevalent throughout the Highlands (Lowe, 1961). The lack of forest cover from continued deforestation forced deer into competition with sheep on pastures (Clutton-Brock *et al*., 1982). Consequently, deer numbers reached critically low levels in the late 18th Century, restricted to 9 'deer forests', tracts of open-mixed forest and hill land (Lowe, 1961). Whilst hunting practises contributed to the population crash, the demand for the sport prompted landowners into action for fear of losing entire deer stocks, and sheep were removed from certain estates (Whitehead, 1964). By 1838, there were 45 deer forests in Scotland, and declines in the profitability of sheep farming made room for increased hunting revenue, and by the early 20th Century there was approximately 1,450,850 ha of deer forest (Clutton-Brock *et al*., 1982, Lowe, 1961).

Following World War II, deer poaching rose to address food shortages (Lowe, 1961). To address this, strict legislation was enforced to address poaching, and uncertainties regarding the status of red deer in Scotland lead to the formation of Red Deer Commission, which provided a standardised framework to evaluate the status of deer (Clutton-Brock *et al*., 1982). From this, the status of red deer populations has been surveyed multiple times throughout the second half of the 20th Century.

Populations continued to increase throughout Scotland, despite resurgence in sheep farming and the increasing enclosure of land for forestry practices (Lowe, 1961). A combination of lack of natural predation, reduced culling and mild winters has contributed to the Scottish red deer population doubling in size from 1950 to 1980 (Clutton-Brock *et al*., 1982) and as such, the carrying capacity of the remaining pine forest has been exceeded and is consequently over-grazed (Baines *et al*., 1994). Currently, red deer number at approximately 260,000 in Scotland, ranging in density from 1 per ha to 120 per ha (Mitchell *et al*., 1977). Whilst Scots pine forest was a dominant habitat of Scotland in 4000 BC, covering an area of approximately 1.5 million ha (Baines *et al*., 1994), currently less than 1% of this original pine forest remains. What remains of the pine forest habitat in Scotland is valued by red deer, as it provides cover when grazing from harsh weather, particularly during the winter months (Baines *et al*., 1994). As such,

incompatibilities between the huge numbers of free-ranging red deer and forestry practices in Scotland are prevalent. The underlying problem stems from the need to maintain a balance in managing resource production whilst minimising the negative impacts on habitats and other land-use needs (Mitchell *et al*., 1977). Specifically, two important yet conflicting motivations for land-use in Scotland are to minimize the damage to agricultural and forestry infrastructure, and to conserve red deer for hunting, meat production and more recently, tourism purposes (Lowe, 1961, MacLellan, 1999). The latter is an increasingly valued source of revenue for Scotland, as traditional agricultural and fishing industries have declined over recent years (Riddington *et al*., 2010).

1.6. THE CURRENT STUDY

A novel land management scheme is planned for Ulva, an island estate in the Inner Hebrides, Scotland, aiming to promote biodiversity on the island whilst moving significantly away from the 'traditional' land use in the region of using sheep as the primary grazer of grassland habitats (Hunter, 1962). The island features short sward habitats which are breeding grounds for rare Lepidoptera species (namely the marsh fritillary *Euphydryas aurinia* and several day flying burnet moth species: transparent burnet *Zygaena Purpuralis*, and the slender scotch burnet *Z. loti*, and one of the main aims of this new management scheme is to promote these habitats through controlled grazing pressures and distribution of red deer, whilst avoiding the negative impacts of deer overabundance.

Z. loti and *Z. purpuralis* are relatively under-studied. The species were previously found throughout the Isle of Mull, Ulva and also the Morvern peninsula on Argyll, but today the population is centralized around south-west Mull and the island of Ulva, inhabiting herb-rich grasslands on basalt soils (Ravenscroft and Young, 1996a). As such, *Z. loti* is classified as a Red Data Book species (Category 3, Rare). *Z. Purpuralis* is listed as 'Scarce' under the UK Conservation status, with populations restricted mostly to the Hebridean Islands and Ireland. On the other hand, *E. aurinia* is well documented (Joyce and Pullin, 2003). The species is listed under the EC Habitats and Species Directive in addition to the Bern Convention, and is listed as a priority species in the UK Biodiversity Action Plan (Smee *et al*., 2011). Whilst the *E. aurinia* maintains a wide distribution in Europe, the total population has been drastically reduced (Joyce and Pullin, 2003, Smee *et al*., 2011). The species is now extinct in Holland and Belgium; 'endangered' in Hungary and Poland; and 'Vulnerable' in Austria, Denmark, Germany, Greece,

Luxembourg and the Republic of Ireland. In particular, the UK population has declined by 55% over the past 30 years (Lewis and Hurford, 1997, Smee *et al*., 2011), remaining only in small pockets of either dry, herd-rich, calcicolous grasslands or damp acidophilus grasslands (Warren, 1994). The Scottish population is largely confined to west Argyll, with other notable populations on the islands of Jura, Islay and Mull (Warren, 1994).

It is anticipated that changing the landscape to promote a more 'natural' ecosystem in appearance, will correlate with an increase in, and redistribution of, tourist activity on the island. Indeed, Scotland is experiencing an increase in recreational activities such as mountaineering, hill-walking and cycling, consequently exposing red deer populations to growing levels of disturbance. Utilizing the red deer as a primary grazing species, it is imperative to understand the impacts that increasing levels of tourism may have on the behaviour and consequently grazing intensity and habitat use of the red deer. The aims of this thesis are to investigate the behavioural responses of red deer towards human activity on Ulva, and how these responses relate to the persistence of the biodiverse short sward habitats. The investigation was addressed in three parts (**Chapters 3-6**, respectively).

Chapter 3. How will varying levels of tourist activity influence red deer behaviour throughout the island?

Throughout a range of taxa, prey species have been shown to exhibit more vigilance when the perceived risk of predation is greater (Frid and Dill, 2002). For ungulates, an increase in vigilance behaviours reduces the chances of predation, generally at the cost of time spent foraging. A variety of factors determine the amount of time and effort wildlife can dedicate to antipredatory behaviours, such as: current body condition dependent on season; the group size; distance to refuge and the openness of habitat, thus improving the success of fleeing and lowering the risk of ambush (Cassirer *et al*., 1992). Additionally, the following conditions concerning the disturbance stimuli itself increase the time and effort spent in anti-predatory behaviours: when the disturbance stimuli approach in a more direct manner (Frid, 2003); have a greater group size (Brown *et al*., 1999); remain at closer proximity (Stankowich, 2008); and occur alongside a greater degree of true natural predation risk (Frid and Dill, 2002). To consider the effects of tourism activities on deer behaviour, key deer behaviours were mapped both spatially and temporally (diurnal and seasonal) in response to tourist activity, at both fine and coarse scales, quantifying the impacts

of tourist activities on red deer throughout the island. Topographic conditions that may affect responses towards disturbance were also considered.

Chapter 4. How will patterns of habitat use throughout the island change in response to differing levels of tourist activity?

Disturbance plays an important role in habitat selection, as the amount of cover provided by habitat decreases detectability from potential predation (Bonenfant and Kramer, 1996). Habitat heterogeneity can reduce the chances of detection through visually obscuring human profiles (Fernández-Juricic and Schroeder, 2003), and topographical features such as ridges and wooded areas can be used by wildlife as cover. This is exemplified by Cassirer *et al*. (1992), in which it was found that in response to skier disturbances, red deer escaped to higher altitudes with nearby wooded areas. Slope is another important habitat feature to ungulates, as it provides vantage points from which to detect predators (Jayakody *et al*., 2011).

Grassland habitats are favoured by red deer, however the species appears more sensitive to disturbance in these areas, possibly due to the lack of cover short sward grassland provides increasing the detectability of red deer to predators (Jayakody *et al*., 2011, Laundré *et al*., 2001). In such a scenario, should the deer then seek cover in either moorland or woodland, a compromise is made in forage quality due to the lesser digestible organic matter available in these habitats. Repeatedly displacing animals from high quality forage can then have long-term implications for production and survival through a multiplier effect (Jayakody *et al*., 2011). Displacing animals from their preferable habitat can also lead to other negative consequences such as increased risk to true predation and overall physiological stress (Duchesne et al., 2000, Sibbald et al., 2011a). It is also worth taking note that displacement to an area featuring lower forage availability could be potentially more detrimental to the animal than the energetic costs involved in escaping from a disturbance event (Cassirer *et al*., 1992). To investigate how tourist presence affects habitat selection, habitat use in response to a series of tourist-activity metrics was investigated at varying seasons, whilst taking into consideration the topographic conditions that may influence the response of red deer to sources of disturbance.

Chapter 5. Can red deer act as an appropriate agent for the maintenance of the biodiverse short-sward habitats on Ulva?

Appropriately managing grazing pressures depends upon the habitats in question and the desired outcomes. Deer grazing can slow or inhibit succession on certain habitats which may be advantageous for land management aims (Warren, 1994). In areas which feature heather, total exclusion of herbivores may not maximise invertebrate biodiversity, as heather has been known to dominate in the absence of grazing, which supports few invertebrate species (Baines *et al*., 1994). However, should one of the relatively few species which heather supports become of significant conservation interest, then little to no grazing would be preferable to maintaining a community of a non-threatened species. Another point to consider is that succession rates vary between plant communities. For instance, tufted hair-grass (*Deschampsia caespitose*) dominated-grasslands can provide suitable habitat for an array of Lepidoptera without requiring any grazing schemes (Smee *et al*., 2011). Contrastingly, *Molinia-Potentilla* dominated mires require regular grazing to prevent the loss of host plants (Warren, 1994). As such, the optimal level of grazing required in maintaining this suitable Lepidoptera habitat varies between different grassland communities (Warren, 1994). Extensive cattle grazing is the traditional approach in maintaining the damp grassland biotypes used by various butterfly species, which benefit from these practices as heterogeneous habitats are created, allowing larvae to bask on the low, open vegetation, whilst tall flowering plants provide for flying adults (Smee *et al*., 2011, Warren, 1994). Modern, more intensive farming methods create a more homogeneous habitat that is unsuitable for the varying needs of many Lepidopteran lifecycles (Smee *et al*., 2011). Sheep have proven to be less suitable for maintaining these habitats than cattle *Bos taurus*, in that they tend to graze more heavily on the herb-rich areas containing foodplants preventing the growth of taller plants used by adults for egg-laying, thereby inhibiting appropriate habitat formation (Warren, 1994).

Grassland management often requires a level of grazing that negates successional changes in the vegetation community, as certain insect species depend upon specific intermediate seral stages (Balmer and Erhardt, 2000). Therefore, the correct grazing intensity achieves a balance between avoiding the successional dynamic of the grassland habitat, whilst also avoiding the negative impacts of over-grazing. Livestock grazing on grasslands impacts the vegetation community and the associated insect community by dramatically altering plant architecture, diversity and growth (Kruess and Tscharntke, 2002). Over

time, intensive grazing can simplify plant diversity by indirectly selecting for grazing-tolerant species (Hunter and Price, 1992), decreasing habitat heterogeneity and in turn reducing the carrying capacity for insect biodiversity (Tscharntke and Greiler, 1995, WallisDeVries and Raemakers, 2001). To maintain a grassland community at a given seral stage, habitat management practices aim to maintain plant diversity by lowering livestock counts and/or altering the grazing periods (Kruess and Tscharntke, 2002). Using *Z. purpuralis* as a bioindicator for the short-sward habitats, *Z. purpuralis* abundances in these areas were related to a series of red deer habitat use metrics to investigate the impacts of deer presence. The relationship of deer presence with favourable conditions for *Z. purpuralis* was also inspected.

Chapter 6. General Discussion

Finally, the general discussion builds upon the previous three chapters and presents a synthesis of the findings to explain the efficacy of red deer as a conservation grazer with respect to the promotion of the short-sward grassland biotopes. Specifically, whether the impacts of human activity on the patterns of deer behaviour and habitat use in the grassland habitats is favourable or detrimental towards the persistence of *Z. purpuralis* was addressed. From this, the thesis provides the first insights into how human-related disturbances can impact upon the ecological landscape by altering the behaviours and patterns of habitat use of a grazer. The implications of this newly researched dynamic are discussed.

CHAPTER 2

GENERAL METHODS (FIELD AND ANALYSIS)

‘Big waves crash on a Hebrides shore,

Horizontal rain slashes the rocks.

There’s no shelter here, not even a crack’

- Tom McMurry

2.1. GENERAL INTRODUCTION

The purpose of this chapter is to describe methods that are common to multiple chapters, thus avoiding any repetition of recurrent methodologies throughout the thesis. Therefore, this chapter will describe the study site, and detail fieldwork and analytical procedures that were necessary in answering the questions proposed in this thesis (Chapters 4-6). Methods specific to data chapters are detailed in each chapter respectively.

2.2. STUDY SITE

2.2.1. ISLE OF ULVA

Fieldwork for all chapters was carried out on the Isle of Ulva, located in the Inner Hebrides in Argyll and Bute, western Scotland (56° 28′ 39.18″ N, 6° 12′ 24.91″ W), (Figure 2.1.). Ulva is approximately 18.4km^2, 8km long from west to east, and 4km wide from north to south, and is horizontally elliptical in shape. On the east coast, Ulva is separated from the Ardmeanach peninsula of Mull by a narrow strait: the Sound of Ulva. On the west coast, Ulva is connected to the island of Gometra by a bridge. The oceanic climate of the region is considered atypical with regards to the overall climatic conditions of the British Isles (Green and Harding, 1983). The Inner Hebrides experience high wind speeds, and rainfall ranging from 55 to 130 inches annually (Boyd, 1983, Ragg and Ball, 1964), yet are very mild – expressed by the minimal variation of temperature both seasonally and diurnally (Boyd, 1983). The Hebrides act as important breeding grounds for many seabirds (Mitchell et al., 2004). The larger islands support populations of red deer, grey seals (*Halichoerus grypus*), common seals (*Phoca vitulina*), and otters (*Lutra lutra*). The main infrastructure on the islands is sheep/cattle grazing, tourism, and pelagic and demersal marine fishing. Forestry on a commercial scale is limited to the small sheltered areas found mainly on the larger islands, whereby Sitka spruce (*Picea sitchensis*) and Scots pine (*Pinus sylvestris*) is harvested. The island is a privately owned estate, but it is managed as a tourist attraction, and public access is allowed throughout most of the island.

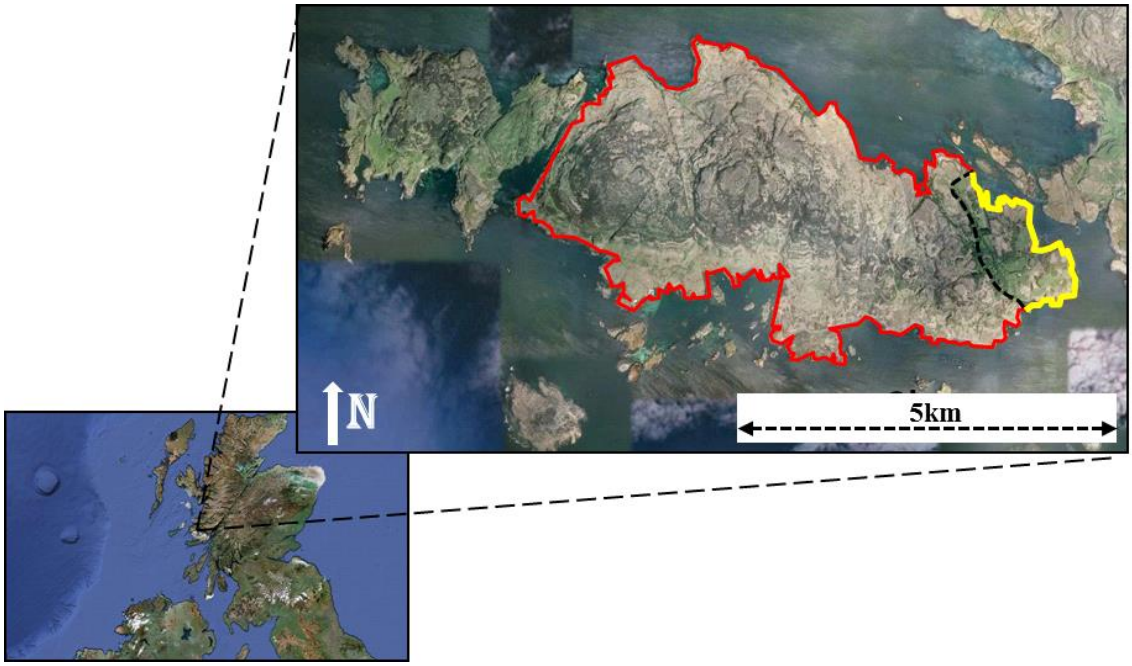


Figure 2.1. The Isle of Ulva: shown is the relative position of the island relative to mainland Scotland, and in its entirety. The area outlined in red and yellow represent the 'Hill' and 'In-By', respectively. The black dotted line represents the separation of these two areas by a deer fence. [*Image © Google Earth]*.

The Isle of Ulva can be defined as being composed of two main areas: namely the 'Hill' area, and the 'In-By' (hereafter referred to as HA and IB, respectively). This division represents on-going land management on the island, in which the IB features comparatively extensive farming practices and associated infrastructure. As such, there is a distinct change in topography between the two areas. The HA is characterized by an altitudinal change in habitat types. At sea level, coastal herb-rich grasslands dominate with bogs occurring intermittently throughout. Sub-montane basalt outcrops denote the upper limit of these grasslands, above which heather/bracken mosaics occur throughout the entirety of the higher altitudes of the island (e.g. 50 to 300mamsl) of the island. This trend is most apparent on the south-side of the HA; the north side exhibits the same pattern albeit in a less distinctive and more gradual change. There are two small yet notable areas of mixed woodland in the HA, both found at the coastal level on the north and south sides of the island. The IB exhibits little altitudinal variation, ranging from 1 to 65 mamsl, and the ground flora is almost completely composed

of pastoral short-sward grasslands, and features comparatively extensive coniferous and open-mixed woodlands throughout. The HA and IB are approximately 17km^2 and 1.4km^2, respectively.

The HA and IB are separated by a purpose built deer-excluding fence, and red deer inhabit both areas. Consequently, two populations of red deer are effectively maintained on the island. However, it is assumed that a degree of migration between the two populations can still be achieved from individuals swimming from one area to the other. Indeed, red deer have been observed to swim the crossing that divides Mull from Ulva, which is comparatively more arduous than swimming between different sections of coastline on Ulva (pers. corr J Howard). Due to this migration, the exact numbers of the red deer in each area is unknown, but it is assumed that substantially greater numbers inhabit the HA, due to its relatively large size and coupled with anecdotal information. Deer population counts in the HA is qualitatively assessed by the landowners on a yearly basis, and the most recent count yielded an estimate of 350-400 deer (per. corr. J. Howard).

Visitors have access to the island from March to September, inclusively. This period is hereafter referred to as Tourist season (T), and dates falling outside of which comprises the Non-Tourist season (NT). Visitor access to the island is conducted by a ferry which crosses from Mull and terminates at a small slipway in the IB on Ulva. Given that the Inner Hebrides area is popular in the summer season with activities such as kayaking and yachting, it is also possible for tourists to access Ulva at alternative locations along its coastline. A network of paths exists on Ulva, which facilitate movement for tourists throughout the island (see Figure 2.2). All path systems in the IB were surfaced, whereas the HA featured both surfaced and unsurfaced paths. As the IB has a much smaller area than the HA and acts as the main entry point for tourists, it is assumed that the tourist density in this area is higher than the HA.

A number of day-flying zygaenid moths inhabit the short-sward herb-rich grasslands, found on the south and southeast facing slopes found on the southerly coast of the HA. Species include: the 6-spot burnet *Z. filipendulae*; *Z. loti* and Z. *purpuralis*. These burnet species overlap in range considerably, as do their respective food-plants, and imagos of all three species have been observed intermittently throughout the HA southerly coastline (pers. corr. T. Prescott). *Z. purpuralis* exists in metapopulations that fluctuate in size with each generation, and are mainly centred on southern

grassland slopes in the HA (J. Howard per. comms.). Whilst *Z. loti* imago forms have been documented on the southeast coastline in the IB, no established populations of any of the three burnet species are thought to occur in the IB (J. Howard per. comms.).

2.3. FIELDWORK AND ANALYTICAL PROCEDURES

2.3.1. STUDY SITES WITHIN ULVA

Data collection within the HA was restricted in range from the central portion of the island, extending towards the southerly/south-easterly side, in order to relate deer behaviour (**Chapter 3**) and habitat use (**Chapter 4**) to both the path networks and potential *Z. purpuralis* habitat (**Chapter 5**). Red deer behavioural data collected in the IB was restricted to grassland areas. This decision was undertaken with regards to practicality, as approaching red deer from within woodland increased the likelihood of the observer being detected and causing the deer to flee. As **Chapter 4** was focused on investigating the habitat use of red deer in the same areas that behavioural observations were undertaken, the respective data collection was also restricted to non-woodland habitats within the IB.

2.3.2. CALCULATING PATH DISTURBANCE METRIC

All GIS-related analyses detailed throughout the PhD were carried out in ArcGIS 10.1. (ESRI, 2011). Statistical analyses performed in **Chapters 2** and **3** required a metric that quantified the disturbance associated with the path systems. To create this metric, it was necessary to obtain the cartographic information of the path systems in order to create polygon in ArcGIS 10.1. that represents the spatial dimensions of the path systems. Initially, the entire path systems were traversed by foot whilst simultaneously recording coordinate positions with a GPS unit every 3 seconds. Path mapping was conducted from 10 April 2013 through to 17 April 2013. These coordinate positions were then transformed into a linear feature using the 'Points to Line' function found within the Data Management toolset. A 1m buffer was then calculated around the line, to replicate the width of the path. Paths were separated into surfaced and unsurfaced paths. Surfaced paths are very conspicuous, and are typified by the complete replacement of vegetation with construction aggregate or gravel.

Unsurfaced paths were less distinct, and were formed from the compression of vegetation from repetitive footfall. As unsurfaced paths were less obvious, they were way-marked with small wooden posts.

To quantify the tourist traffic of different paths on Ulva, 6 Reconyx Hyperfire trail cameras were positioned at 20 locations throughout the path system (see Figures 2.2. for IB and 2.3. for HA) from the 10th June 2015 to the 13th July 2015, and a rotation scheme was maintained to ensure that the traffic at each location received similar amounts of coverage over the course of the data recording period. The path system was delineated into sections, and each section was attributed a traffic metric, which was the recorded total number of tourists captured on a given path. In the IB, path delineation was based on the intersection of paths.

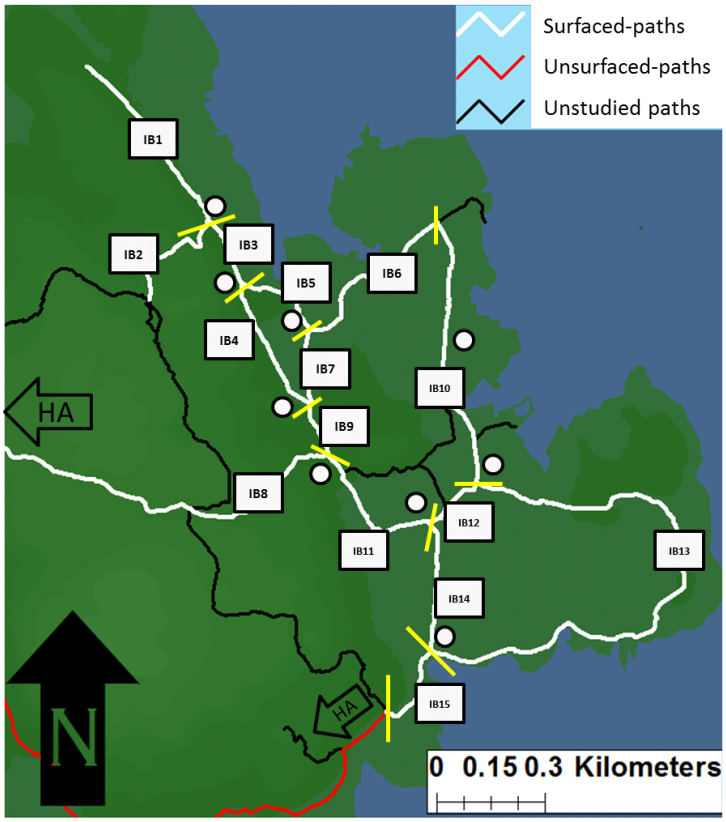


Figure 2.2. The path system and camera trap positions in the IB. Unstudied paths are coloured black, studied surfaced paths are coloured white, and studied unsurfaced paths are coloured red. White points indicate camera positions. Path segments are delineated where intersections occur, and this is highlighted by the yellow markings. Path segments are classified according to the alphanumeric combination in white boxes. Arrows with 'HA' inset show which paths lead towards the HA.

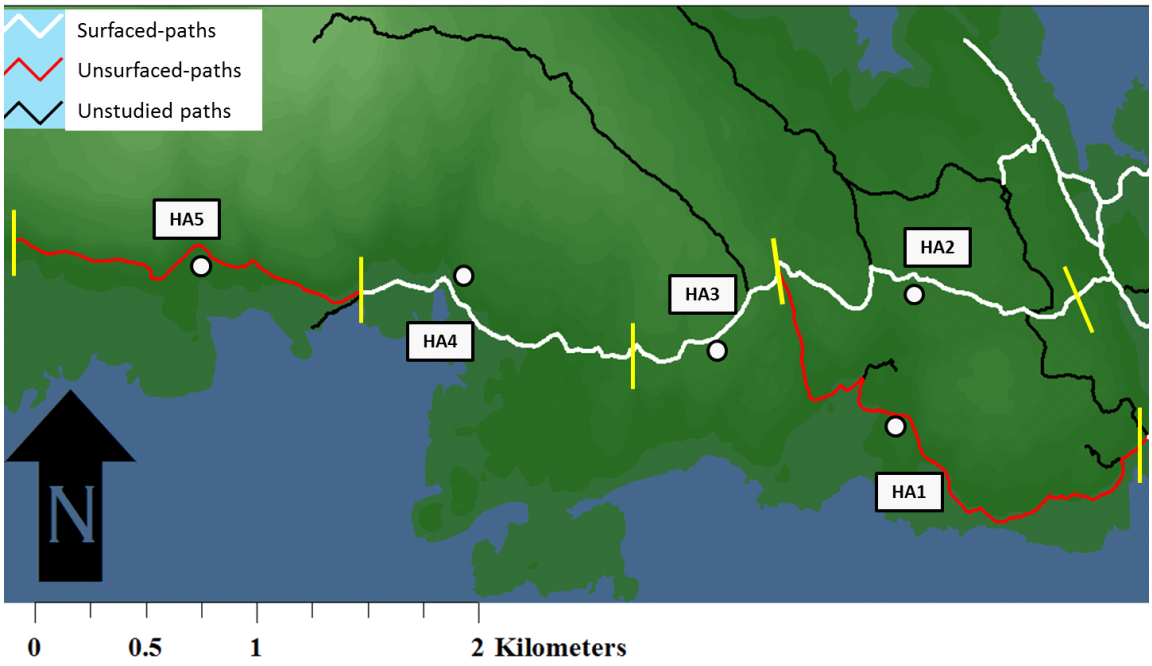


Figure 2.3. The path system and camera trap positions in the HA. Unstudied paths are coloured black, studied surfaced paths are coloured white, and studied unsurfaced paths are coloured red. White points indicate camera positions. Yellow markings indicate where path segments were delineated. Path segments are classified according to the alphanumeric combination in white boxes.

The same approach could not be applied to the long, uninterrupted path systems in the HA, and as such, path delineation was made according to notable sites visited by tourists that potentially act as final destinations (J. Howard per. comms.). Efforts were made to place cameras at path intersections, and positioned with the aim of capturing all paths that comprised the respective intersection, thus maximising possible observations for multiple paths simultaneously. Total recording days for each path section are shown in Table 2.1. The total number of visitors observed on a given path throughout the entire recording period was used as the disturbance metric.

Table 2.1. A summary of the traffic recording results for each of the designated path segments illustrated in Figures 2.2 and 2.3. Type refers to whether the path is a surfaced or unsurfaced path. Total traffic refers to the total number of observed visitors throughout the total no. of recording days. The camera position refers to the location of the camera from which the respective path was observed.

Path	Type	Total Traffic	Total no. of recording days	Path length (m)	Camera Position (Decimal Degrees)
HA1	Unsurfaced	1	33	2356	-6.173164, 56.468286
HA2	Surfaced	805	33	1006	-6.174539, 56.473761
HA3	Surface	359	33	1002	-6.179542, 56.473117
HA4	Surfaced	150	33	1461	-6.206945, 56.473617
HA5	Unsurfaced	9	33	1597	-6.225172, 56.472807
IB1	Surfaced	131	27	558	-6.163700, 56.480789
IB2	Surfaced	83	28	379	-6.163700, 56.480789
IB3	Surfaced	366	27	214	-6.163700, 56.480789
IB4	Surfaced	91	27	378	-6.163890, 56.478593
IB5	Surfaced	507	28	217	-6.163890, 56.478593
IB6	Surfaced	626	27	536	-6.159047, 56.477566
IB7	Surfaced	343	27	229	-6.159047, 56.477566
IB8	Surfaced	948	27	290	-6.158530, 56.473633
IB9	Surfaced	204	27	138	-6.158530, 56.473633
IB10	Surfaced	585	24	508	-6.152477, 56.477263
IB11	Surfaced	183	27	395	-6.158530, 56.473633
IB12	Surfaced	252	27	108	-6.150473, 56.474664
IB13	Surfaced	196	27	1720	-6.150473, 56.474664
IB14	Surfaced	252	33	401	-6.152662, 56.470307
IB15	Surfaced	252	33	139	-6.152662, 56.470307

2.3.3. HABITAT CLASSIFICATION CATEGORIES

Habitat type was considered in the analyses presented in **Chapters 3** and **4**. The difference habitats found on UIva were categorised into the following distinct categories: **'GH'** - grass/heather mixed: generally short-medium sward grasses such as *Holcus mollis* and *Molinia spp.* with a large *Calluna vulgaris* or *Erica cinerea* component; '**HMG'** - heather/moss/grass mixed: similar to the GH

habitat, but with less *C. vulgaris* and *E. cinerea*, and a large moss component.; '**B**'- bog: patches of tall reeds and rushes with a very dominant moss component; '**H**' - heather domination: complete cover of *C. vulgaris* or *E. cinerea*, or a mixture of both; '**BR**' – bracken domination: complete cover of *Pteridium aquilinum*; '**GB**' – bracken/grass mixed: near dominance of *P. aquilinum* over short or medium-sward grasslands; '**G**' – grassland: forb-rich short-sward grassland featuring *Agrostis spp*. and *Fescue spp*., with small portions of *H. mollis*; '**RO'** and '**RS**'– rocky outcrop and rocky shore, respectively.

2.3.4. PRODUCING TERRAIN TOPOLOGY RASTER DATASETS

All Chapters required several shared GIS-derived topological metrics. Specifically, terrain topology rasters were involved in investigating red deer behavioural patterns (**Chapter 3**), red deer habitat use patterns (**Chapter 4**), and *Z. purpuralis* habitat use patterns (**Chapter 5**). Additionally, metrics for the proximity and visibility of the path systems in Ulva were derived from GIS analyses and applied in **Chapters 3** and **4**.

Terrain topology rasters include: altitude, slope and aspect. Initially, a 5m resolution Digital Terrain Model raster (DTM) of Ulva was obtained from NEXTMap, a DTM dataset representing the entirety of Britain produced by Intermap. The DTM provided altitude data (Z axis) at a 1m accuracy, from which 5m resolution raster datasets of slope and aspect were calculated using the Slope and Aspect functions found in the Surface Analysis toolset in ArcGIS 10.1.

The investigation of habitat use patterns in **Chapters 4** and **5** necessitated a land cover map that differentiated the habitat types found in the HA. To create a thematic land cover map, a multi-band RGB (red, green and blue) image of the target area is required, as the image classification process uses the band combinations of RGB in an image to differentiate land cover types. Initially, a high-resolution TIFF file of Ulva was sourced from Google Earth. This multi-band image was exported into ArcGIS 10.1., and georeferenced onto the British National Grid system, whereby the coordinates of distinctive coastline features and the path systems acted as control points. Image classification tools (enabled with the Spatial Analyst extension) allowed for the creation of signature files, which are examples of the spectral signatures (specific RGB combinations) of the different habitat types in the image file, collected by the user. Signature files were collected for 'short-sward

grassland', 'bracken', 'bog', 'poor-grassland/moss mosaic', 'heather', 'rocky shore' and 'water'. Visually distinct habitats possess unique band combinations. The final land cover raster was produced from extrapolating these example signature files across the entire image i.e. raster cells were created from assigning the correct signature files depending on the spectral signature of the underlying image file in a given area. Raster cell size was 5m. The performance of this process was visually inspected by comparing the multiple signature files for each unique band combination determined by the user plotted in scatterplots. Extensive overlap of band combinations implies that the signature files collected by the user were poor examples of the respective habitats, and resampling of the RGB combinations is required. The resulting land cover map produced from this process is shown in Figure 2.4.

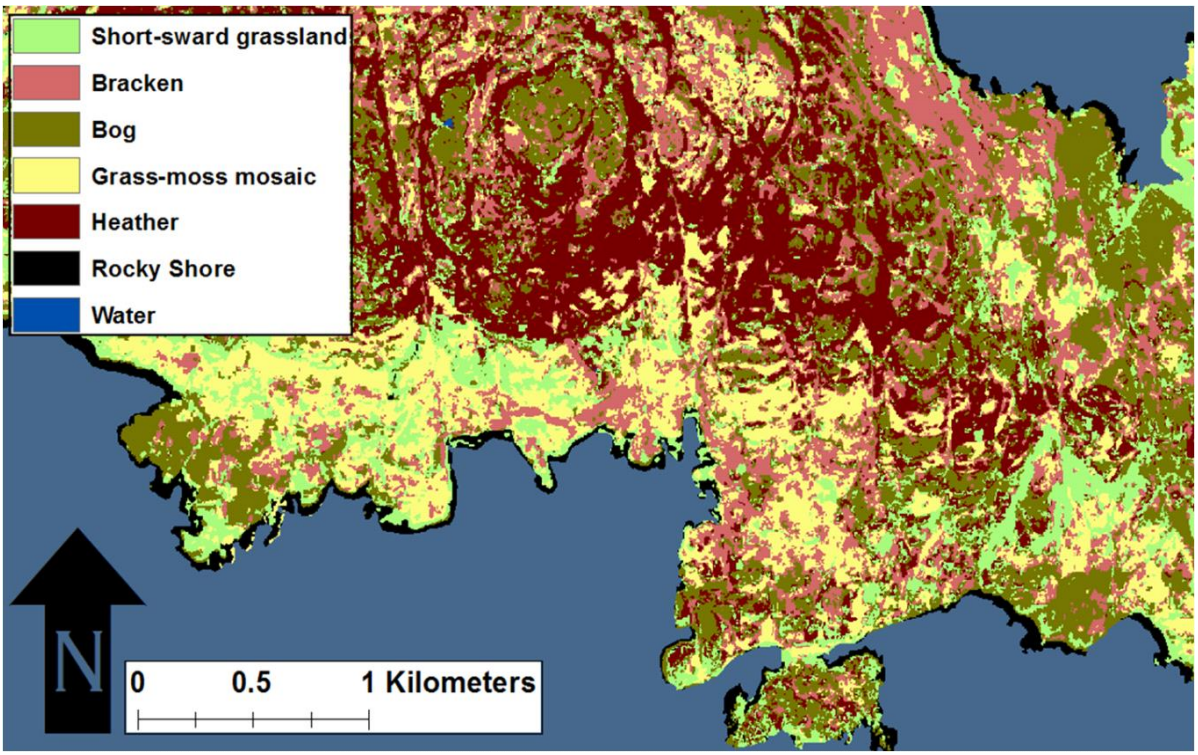


Figure 2.4. Thematic land cover raster of the HA, produced from a supervised image classification process using spectral signatures (i.e. reflectance values) obtained from satellite imagery, required for analyses in **Chapter 4** and **5**. Original satellite imagery was taken outside of growing season, and therefore bracken was easily identifiable in exhibiting a contrasting pink signature. Habitat types are detailed in legend provided. Raster cell size = 5m.

2.3.5. PRODUCING PATH DISTANCE AND PATH VISIBILITY RASTER DATASETS

The investigation of red deer behaviour and habitat use patterns in **Chapters 3** and **4** required the creation of a distance to path raster and a path visibility raster for both sites. Unsurfaced and surfaced paths vary substantially in conspicuousness, and potentially impact upon wildlife differently. As such, the distance to path and path visibility rasters were created twice: for all paths, and surfaced paths only. Analyses pertaining to each are termed PATH1 and PATH2, respectively.

Firstly, a distance to path raster was created from the 'Euclidean Distance Raster' function found within the Spatial Analyst toolset, using the digitized path network polygon as the source from which Euclidean distances were calculated. This process resulted in the production of a raster dataset of Ulva, in which every cell contained a value of the Euclidean distance to the most proximate part of the path. Distances are measured in the projection units of the raster (1m cell size).

A path visibility raster was created from the 'Viewshed Analysis' function found within the Spatial Analyst toolset. This function creates a raster dataset, the cells of which are attributed a value that represents the visibility of a given feature from a given cell depending on the surface elevations of the terrain, provided by the DTM. In this case, the visibility of each path segment was required separately, and this analysis was therefore repeated for each path segment, thus creating 20 visibility rasters in total. Cell values represent the number of cells that a given path can be seen from. The context for this analysis relates deer behaviour and habitat use to the visibility of the nearest path given the position of the deer, and as such, a 1.5m above-ground-level factor was incorporated into the calculations to account for the approximate vertical height achieved by a scanning deer (Renaud *et al*., 2003).

2.3.6. TIMES AND DATES OF OBSERVATIONS

Fieldwork was undertaken at both T and NT seasons from 2013 to 2015. Specifically, fieldwork was undertaken from 10 April 2013 to 20 May 2013 (T); 1 September 2013 to 26 September 2013 (T); 1 November 2013 to 1 December 2013 (NT); 20 April 2014 to 6 June 2014 (T); 20 August 2014 to 23 September 2014 (T); 1 February 2015 to 1 March 2015 (NT); 24 May 2015 to

14 July 2015 (T); and 29 November to 23 December 2015 (NT). Dates specific to a particular aspect of fieldwork which are unique to an investigation will be detailed in respective Chapters.

CHAPTER 3

THE BEHAVIOURAL RESPONSES OF RED DEER TO CURRENT MANAGEMENT PRACTICES AND TOURIST DISTURBANCE

'And remember the night is for hunting,

and forget not the day is for sleep'

- Rudyard Kipling

3.1. INTRODUCTION

To quantify the behavioural impacts of human disturbance, behavioural responses (e.g. the likelihood of fleeing) and behavioural changes (e.g. differences in time budgets) are commonly used as indices of sensitivity to disturbance stimuli (Stankowich, 2008). Flight initiation distance, or the distance from the potential predator at which the prey begins to flee, is often used as a metric in assessing behavioural responses to human disturbance (Eason *et al*., 2006, Stankowich, 2008). However, this approach has received a mixed reception (Beale and Monaghan, 2004a, Gill et al., 2001b), as using a single behavioural metric such as flight distance is insufficient as a standalone indicator of sensitivity to human disturbance; it is also essential to take into account a variety of factors (Stankowich, 2008). The vulnerability of an animal at a given time can be considered to be the product of a number of physiological and environmental variables that vary both spatially (e.g. forage availability, proximity to refuge) and temporally (e.g. seasonality of food resources, life history and developmental changes). These factors are important for an animal when making trade-off decisions. If an animal is in good body condition with alternative forage or refuge nearby, it can bear the costs of changing its behaviour in response to a disturbance stimulus. If the refuge availability factor was ignored, the herd inhabiting the area with no refuge could be perceived to be more habituated to the disturbance stimuli, but in actuality the option of fleeing to refuge is costlier and therefore less readily triggered by the disturbance stimuli. For example, a herd of ungulates foraging in an area with available refuge will, all else being equal, flee more readily in response to a disturbance stimuli than a herd of ungulates foraging in a site with no refuge available to flee to (Frid, 1997, Gill *et al*., 2001b).

The effect of multiple factors may not present a simple additive relationship, but rather wildlife responses may be partly driven by a multiplicative relationship of these factors. A comprehensive review found a high degree of heterogeneity in the effect size of these factors, suggesting that animal responses are likely to be influenced by the interactive effects of the many factors involved (Stankowich (2008). These interactive effects have been poorly studied, and the relative importance of the multiple factors driving responses to disturbances is ignored in many studies (Petraitis *et al*., 1996, Stankowich, 2008). However, interactive effects have indeed been found to significantly influence anti-predatory decisions (Cooper *et al*., 2003, Frid, 2003, Stankowich, 2008). For example, Frid (1997) found that Dall's sheep (*Ovis dalli*) exercised less vigilance in larger herds, but this relationship weakened with increasing

proximity to cliffs. In accounting for interactive effects between disturbance metrics and other environmental conditions, more realistic predictions can be made for understanding prey responses to disturbance stimuli.

3.1.1. RESEARCH AIMS AND OBJECTIVES

Therefore, the objectives of this chapter are twofold: 1) to assess how the activity patterns exhibited by red deer at the individual scale may be influenced by varying levels of exposure to a combination of metrics of anthropogenic disturbance, and 2) to determine if there is any association of red deer behaviour with the topographical and vegetative characteristics of Ulva.

Objective 1: Ulva provides a unique situation for researching how red deer respond to anthropogenic disturbance, as the island is characterised by two distinct environments that vary dramatically in terms of exposure of red deer to sources of anthropogenic disturbance. Whereas the IB features a dense network of paths and regular anthropogenic disturbance, and is a small, enclosed area with many man-made barriers (e.g. housing, walling, fencing), the HA area features comparatively infrequent disturbance and larger open spaces, allowing for less exposure to sources of anthropogenic activity. As such, the red deer inhabiting the IB are likely to experience a greater degree of disturbance than those residing in the HA area (J. Howard per. comms.). Regular anthropogenic activity has been found to coincide with a moderation of anti-predatory behaviours in wildlife; breeding grey seals (*H. grypus*) inhabiting a regularly disturbed mainland colony were observed to spend less time engaged in alert behaviours than conspecifics inhabiting isolated island colonies (Bishop *et al*., 2015). From this, it is anticipated that red deer in the IB will exhibit a form of habituation (the progressive reduction in reactive behaviours towards anthropogenic stimuli) whilst deer in the HA will exhibit heightened anti-predatory behaviours and reduced foraging behaviours in response to the relatively infrequent disturbance. Similarly, the activity budgets of reindeer (*R. tarandus*) have been found to adjust in favour of vigilance by decreasing foraging times in the presence of tourists (Duchesne *et al*., 2000).

To test these hypotheses, activity budgets of foraging and anti-predatory behaviours of red deer were recorded in relation to a series of spatial metrics associated with the path systems. Beale and Monaghan (2004) found that behavioural responses to visitors vary both with the number of visitors present and the distance from those visitors, which contrasts with previous conservation practice to

standardize disturbance regimes by considering the metric of distance alone. In the current study, the disturbance metrics accounted for are: 1) proximity of the closest path, 2) visibility of the closest path as governed by topology, and 3) the extent of traffic volume of the closest path. This process was applied to deer residing both the IB and HA area with respect to two temporal scales: seasonal and diurnal. Given that red deer in the HA are expected to be less habituated to anthropogenic disturbance than in the IB, it is predicted that vigilant behaviours will undergo stronger seasonal and diurnal fluctuations in the HA than in the IB. In exchanging foraging behaviours for anti-predatory behaviours during tourist visiting times, it is anticipated that red deer will exhibit compensatory foraging in the absence of tourists. Specifically, red deer in the HA will exhibit a reduction in anti-predatory behaviours towards the path systems is expected both during non-tourist season and at night. As IB deer are expected to exhibit a stronger degree of habituation than HA deer, it is anticipated that anti-predatory behaviours towards path systems will vary less seasonally and diurnally.

Objective 2: Habitat features can affect aspects of ungulate behaviour (Mysterud *et al*., 1999), particularly when cover is formed from topography or vegetation, which can affect anti-predatory vigilance behaviours (Creel *et al*., 2005), herding tendency and circadian rhythms (LaGory, 1987). On Ulva, the HA and IB areas vary markedly in terms of topography and habitat types, and both areas offer potential cover to red deer through different means: the HA features altitudinal variation that creates several vantage points throughout the landscape, whilst the IB provides vegetative cover through extensive woodland. Previous work has shown that increased proximity to refugia such as woodland or thick heather can reduce the behavioural responses of red deer towards human disturbance (Jayakody *et al*., 2008, Stankowich, 2008). Additionally, ungulates have been shown to express varying reactions towards the altitudinal positioning of tourists. For example, tourists induced a much greater flight response in Nubian Ibex (*Capra nubiana*) when approaching the animals from up slope, presumably blocking potential escape routes (Tadesse and Kotler, 2012). The red deer residing in the HA area are also known to flee to higher altitudes once disturbed (pers. corr. J Howard). Consequently, the influence of terrain and habitat types on red deer activity budgets was investigated. It was predicted that deer residing in the HA area will express less anti-vigilant behaviours when positioned on HA slopes, as these habitats provide good vantage for detecting tourists, and close refugia are provided in the form of higher altitudes. Similarly, it is predicted that deer will express less vigilance when positioned in dense vegetation, such as bracken and heather

habitats. In the IB, it was predicted that deer residing in the IB will lower the time spent in vigilant behaviours when occupying areas close to woodland. To test these hypotheses, activity budgets at the individual scale were recorded throughout in both areas in relation to the following environmental metrics: habitat type, altitude, slope and aspect.

3.2. METHODS

3.2.1. BEHAVIOURAL OBSERVATIONS PROTOCOL

Observations were conducted at two scales: scan sampling for herd behaviour, and focal sampling for individual behaviour. Herd behaviour was investigated by conducting instantaneous scan sampling (Altmann, 1974) at 10 min intervals upon spotting a herd by an observer situated in a hide or on foot; herein termed 'fixed observations' and 'transect observations', respectively. In both cases, the behavioural definitions listed in the ethogram were applied to each individual deer, starting from the left-side of the herd and progressing towards the right, until a behavioural category was applied to all functionally visible individuals. A herd was defined as a group of red deer, the members of which are typically closely arranged and generally exhibit a mutual direction of travel. Sometimes, the timing of a scan observation coincided with instances of herd fusion or fission, making herd delineation problematic; in those cases all individuals were considered to belong to a single herd, because the behaviour of any individual could be affected by the proximity of the whole group. For all scan samples the following herd information was recorded: sex composition of the herd, herd size, and the age class (adult or calf) of each individual. The maximum group size counted was used for analysis. Both fixed and transect observations were conducted because shelter afforded by the hide allowed for long observation bouts in the inclement weather, whilst transect observations improved coverage of the area.

Fixed observations were carried out by instantaneously recording a scan sample upon spotting a group of deer from a hide. Hide locations are shown in Figure 3.1. and hide dimensions are detailed in Figure 3.2. Between each scan sample, a 5-minute focal sample was performed on a member of the group if visible. Individuals were picked on a left-to-right basis. A bespoke VBA (*Visual Basic for Applications*) program was used to record direct focal samples of deer behaviour. The data-entry screen was customized to allow for efficient focal sampling; a pressure-sensitive screen/pen-based user-interface

reduced the time spent entering behavioural data and maximised the time spent observing. Focal samples were attributed the same position data as the previous scan sample.

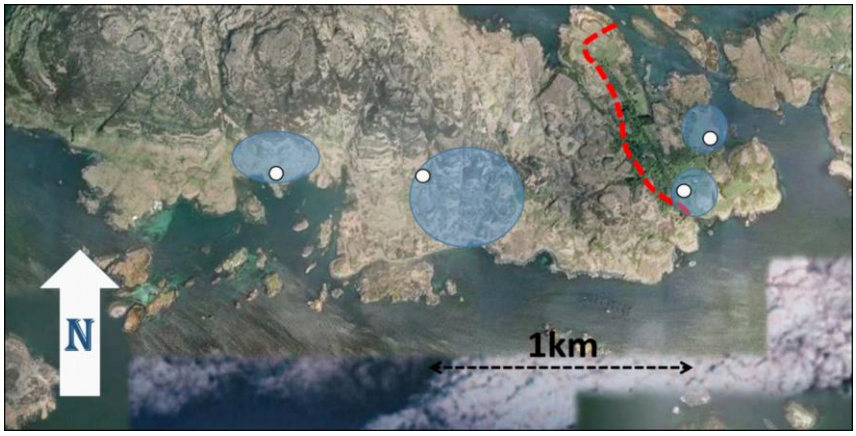


Figure 3.1. Hide positions (white circles) with the approximate fields-of-view (translucent blue areas) shown throughout the HA and the IB (delineated by red dotted line). Exact hide positions given in decimal degrees from left to right are: 56.471300, -6.218132; 56.472916. -6.196331; 56.471778, -6.154789; and 56.477088, -6.157535.

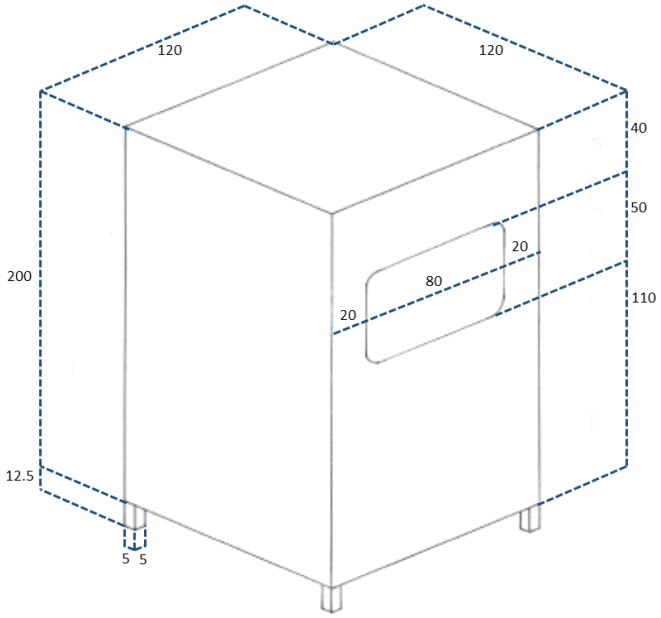


Figure 3.2. Dimensions of the hide structure created for carrying out focal observations, all measurements are given in centimetres. The viewing window was 50x80cm, and so the field-of-view was restricted on a lateral basis when conducting day-time observations. Nocturnal observations benefitted from visualising the thermographic display remotely on a laptop, allowing for a 360° field of view.

Transect observations were performed by firstly walking random routes along the paths on the island. Positions throughout the paths were identified as suitable for conducting observations on the basis that the position provided a vantage point from which red deer could feasibly be spotted at a non-intrusive

distance. Upon reaching a site, the observer would spend 15 minutes awaiting the presence of red deer to enter the surrounding area. If a herd of red deer entered the area within 15 minutes, an instantaneous scan sample (as previously described) was performed, and repeated every 10 minutes until the deer moved out-of-sight. If, within the 15-minute period, no deer enter the site, the observer proceeds along the path to the next designated position and repeats the process. To increase the coverage of deer behaviour throughout the island, opportunistic sampling also occurred in the instance that deer were sighted whilst traversing the path. No focal sampling was recorded during any part of transect scans, as the extra equipment required was deemed unsuitable for recording whilst on foot.

A GPS unit, compass and rangefinder were used to determine the coordinates of the location of each scan sample. Wind speed and rainfall were recorded *in situ* at the start of every scan observation. A Kestrel 1000 Anemometer was used to record average wind speed at a 0.4m/s resolution. Rainfall was categorised as absent/present. The habitat featuring the herd nuclei was recorded, as described in **Chapter 2**. All scan and focal sampling were conducted using a spotting scope (Swarovski (20 x 80)) and hand-held binoculars (Nikon (10 x 42)). Repeat sampling of individuals was likely with this method, and so the most deer observed in one location was used as the sample size.

Although circadian rhythms are a topical area of research, studies that have investigated the nychthemeral (24 hour period) activity patterns of wild animals have typically relied upon indirect methods of data collection such as radio-telemetry (Beier and McCullough, 1990, Georgii, 1981), or motion-sensitive accelerometers (Adrados et al., 2003b, Moreau et al., 2009). Data collected in this manner is arguably limited as information is often recorded at from small sample sizes (Pépin *et al*., 2006, Pépin *et al*., 2009). Additionally, enforcing invasive procedures of attaching and retrieving data recording equipment from specimens can potentially incur stress and add disturbance, thus altering the behavioural states that might be recorded. This is an important point, as it may influence flight distances and tolerance to human activity. To date, no studies have conducted 24 hour observations on wild free-ranging red deer, and therefore how responses in wildlife may vary to anthropogenic disturbance throughout the 24-hour scale is unknown. Through the implementation of thermal imaging equipment, it is possible to conduct 24-hour observational recording of red deer 24-hour behavioural patterns. At night, observations were made using a FLIR 640 thermal imaging scope fitted with a 100mm lens with x2 magnification.

3.2.2. TIMES AND DATES OF OBSERVATIONS

Behavioural observations were undertaken during both tourist and non-tourist seasons (henceforth referred to as T and NT, respectively) from 2013 to 2015. Deer were observed opportunistically, and efforts were made to observe deer throughout the nycthemeron and in both sites. Decisions on whether to conduct observations from either hide or from transects were based on weather, opting for transects in times of poor visibility, owing to the potential to approach deer more closely for observations.

Table 3.1. Time chart of fieldwork dates from 2013 to 2015. Each month is separated into 4 blocks, roughly corresponding to weeks. Months are arranged from chronologically relative to season. Reading from left to right and from top to bottom, specific dates are 10 April 2013 to 20 May 2013; 1 September 2013 to 26 September 2013; 16 November to 5 December 2013; 20 April 2014 to 6 June 2014; 20 August 2014 to 23 September 2014; 1 February 2015 to 1 March 2015; 24 May 2015 to 14 July 2015; and 29 November to 23 December 2015.

Year	T					NT				
	APR	MAY	JUN	JUL	AUG	SEP	NOV	DEC	FEB	MAR
2013	HO					HO	HO/JD			
2014	HO/JD					AV/HO/JD				
2015	HO/JD							HO	HO/JD	

3.2.3. BEHAVIOURAL ETHOGRAM

Distinct behavioural categories were defined from preliminary behavioural assessments conducted on captive red deer maintained on a private estate (Raby Castle, Co. Durham, England, 54.59350N, -1.79600E). All behaviours catalogued in the ethogram were chosen on the bases that they are mutually exclusive and can be accurately identified at a distance by observing a specific combination of simultaneous behavioural indicators displayed by the target animal.

Head-raised behaviour.

A.1 Ruminating: This category is used to denote a target animal which is stationary and displays a raised head whilst chewing. Additionally, a key diagnostic indicator of this category is that the ears are not erect.

A.2 Walking: Simple locomotion category in which the head is raised, and at least 2 legs are on the ground at all times.

A.3 Running: Locomotion characterized by a faster pace than walking, to the extent that all legs are off the ground at times.

A.4 Alert: Similar to ruminating in that the target animal is stationary with a raised head, but with the notable exceptions of displaying erect ears that exhibit darting movements, and the target animals do not masticate. Deer visibly scans the environment with quick purposeful movements of the head.

Foraging behaviour

All cases in which the target animal is grazing ground flora or browsing from shrubs/trees, whilst slowly moving forward to position mouth over new forage.

Resting

Lying posture is adopted, whilst mastication is continuous. Target animal may groom or inspect ground intermittently.

Other

All cases in which target animal displays a behaviour not described by the previously listed categories. Typically, this was realized in numerous and unique conspecific interactions, such as practice mating, antagonistic displays, or excessive grooming, all of which were deemed to be too rare for inclusion in data collection.

3.2.4. ENVIRONMENTAL DATA

Mean daily temperature, sunrise and sunset data for each recording day was retrieved upon request from the UK Meteorological Office; Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current), recorded at the closest weather-observing station in Dunstaffnage (Src ID 918), 56.4505N, -5.43859E. The aspect, slope and altitude relating to the position of each scan recorded was retrieved from post-fieldwork GIS analyses, whereby the coordinates recorded for each scan was used to digitize scan positions with ArcGIS 10, and subsequently using the 'Extract to Point' tool, the values from the respective topographical raster layers (detailed in **Chapter 2**: sections **2.2.3**) were attributed onto the overlaying scan positions.

3.2.5. OBSERVER ID

An additional observer increased the chances of opportunistic observations, and allowed for simultaneous recording from both hides or from a given hide and transects. As such, observer ID was

noted for each observation. HO was the chief observer for all field seasons. All field assistants were trained in the identification of behaviours and observational protocols by shadowing HO for one week on fieldwork before collecting data independently. JD collected data in November 2013, April 2014, August 2014, February 2015 and May 2015, and AV collected data in August 2014. The presence of observer bias was investigated by including observer ID in preliminary analyses.

3.2.6. CALCULATING DAY/NIGHT POSITION

To account for changes in the amount of daylight at a given time of day throughout the year, the time of each scan was converted into a proportion that denotes the position in the range of daylight (between sunrise and sunset) in a given day, and for scans recorded during the night, the position on the range of twilight (between sunset and sunrise) in a given night. By converting the times of scan recording, sunrise and sunset into decimal times, the time of a given scan *s* can be expressed as a fraction of the period between sunrise (0) and sunset (100) by the following:

$$s = \left(\frac{S - m}{M - m}\right) \times 100. \quad (1)$$

Treating the period between sunrise and sunset as a range of values, sunrise *m* represents the minimum value, sunset *M* represents the maximum value, and *S* represents the time taken at a given scan. Observations conducted in the night period were similarly converted into a fraction by the same process, substituting the minimum value *m* for the sunset of that recording day, and the following sunrise is used as the maximum value *M*. To allow both day and night observations to be analysed on the same scale, a value of 1 was added to the night observations, therefore day observations ranged from -1 (sunrise) to 0 (sunset), whilst night observations range from 0 (sunset) to 1 (sunrise of the following day).

3.2.7. STATISTICAL PROTOCOLS

Activity budgets for each behaviour were calculated from the focal samples in order to quantify the proportion of time each individual spent performing the discrete behavioural categories. As red deer may manage risk by scanning the environment in a manner less obvious than exhibiting pure 'alert' behaviour (Sibbald et al., 2011a), a broad behavioural category was formed from pooling all head-raised behaviours (walking + running + ruminating + alert) in order to quantify the level of 'apprehension' exhibited (Hochman and Kotler, 2007).

The factors driving individual activity budgets for the distinct behaviours recorded were investigated by fitting zero-one inflated beta regression models. The focal observations yielded continuous proportional data, i.e. proportions of time spent in a given behaviour during 5-minute recording bouts, ranging from 0 to 1, inclusively. Ferrari and Cribari-Neto (2004) recommended the use of beta regressions to model continuous proportional data; however, when 0 and 1 values are present in the dataset, it is necessary to transform the data to be between 0 and 1 in order to meet the assumptions of the beta distribution. This introduces the problems of modelling datasets that were not observed and interpreting transformed data. Ospina and Ferrari (2010) proved that transformations are not necessary in this scenario, by showing that zero-one inflated beta regressions formed from mixing discrete distributions can model the probability mass of the continuous component and at 0 and/or 1 values. In summary, zero-one inflated beta regression modelling uses a mixture of sub-models that were used to model the focal data according to three distributions:

- A beta distribution regression that models the expected proportion of time a red deer displayed a given behaviour that is between 0 and 1, exclusive, as a function of a selected combination of independent variables.
- A zero-inflated discrete distribution regression that models the expected proportion of responses in which a red deer exhibited zero time spent in a given behaviour, as a function of a selected combination of independent variables.
- A one-inflated discrete distribution regression that models the expected proportion of responses in which a red deer exhibited a given behaviour which lasted the full 5 minute focal, as a function of a selected combination of independent variables.

HA and IB were analysed separately for the entirety of this chapter, as site was found to be collinear with distance to path, visibility of path, path traffic, altitude, aspect, slope and wind when included as a predictor in the models. To test how the effects of tourism affect grazing regimes of deer by eliciting anti-predatory behaviours, behaviours tested will be limited to foraging and anti-predatory activities. Specifically, the response variable was the proportion of time that individuals spent in the following behavioural categories: ‘foraging’; ‘ruminating’; ‘alert’ and in the pooled behavioural category ‘head-raised’.

Data limitations in the HA dataset dictated that sub-setting the data was a necessary step in order to investigate the effects of all of the predictor variables. To test the effects of the proximity to, and traffic and visibility of the nearest path systems upon observed red deer behaviours, the full HA dataset could not be used because not all paths were measured for these disturbance metrics. Therefore, the HA dataset included only data points from which the most proximate path was measured in terms of traffic and visibility, as detailed in **Chapter 2**, section **2.2.4**. This approach allowed for a thorough investigation of the main effects and two-way interactions of several path metrics on deer behaviour, which were: path proximity, path visibility, and the traffic category of the path. These metrics were also tested for interactions with season. A smoothing term was applied to the path proximity variable, in case it had a non-linear effect upon deer behaviour. Non-path related predictors included were: weekday/weekend category, sex of deer, season, day/night position and herd size. The categorical variables rain and habitat were not included in this analysis due to data limitations, as the smaller dataset could not support the involvement of three categorical variables. This analysis was repeated by exchanging path metrics derived from the surfaced path network with those derived from all paths - including unsurfaced paths (herein termed PATH1 and PATH2 analyses, respectively). All model variations of PATH1 and PATH2 were repeated by interchanging the following behavioural categories as the response variable: foraging, ruminating, alert and head-raised behaviours. To investigate which remaining factors were driving the activity budgets for each distinct behaviour, the full dataset for HA was used which supported the inclusion of habitat as a categorical variable, and also included: weekday/weekend category, sex of deer, day/night position, slope, aspect, herd size, rain category, wind speed, daily average temperature and distance to the nearest path (regardless of whether the most proximate path was studied for traffic and visibility), and the interactive effect of path proximity with day/night position. This interactive term was not included in the PATH1 and PATH2 analyses because the distance to path variable was calculated for every focal and so benefitted from being tested in the full HA dataset. A smoothing parameter was included for day/night position, as any effect of the nychthemeral cycle was likely to be strongly non-linear. To attain a sufficient number of habitat categories within the HA, similar habitats with insufficiently low occurrences were pooled into the following: ‘Bracken Mosaic’ (BR and BG); and ‘Heather-Mosaic’ (GH, H and HMG). Categories G and B were observed at high occurrences and were thus unaltered.

Regarding the IB, only one set of predictors was modelled on the full dataset, as the issues affecting analysis of the HA dataset did not affect the IB dataset. Grass was the only habitat recorded for all observations in the IB and, consequently, habitat as a predictor was removed from the analysis, removing the need to analyse the path metrics and habitat types separately. Furthermore, the delineation of surfaced and unsurfaced paths was not applicable for the IB dataset since all of the paths in the IB are surfaced. With the exception of habitat, all other predictors present in the HA models were included when modelling the IB data. All possible two-way interactions of distance to path, path traffic category, and path visibility were tested. Additionally, all path metrics were tested for interactive effects with season and day/night position. All model variations of the IB dataset were repeated by interchanging the behavioural categories as the response variable.

Predictor variables included in final models for focal analyses were selected following the Akaike's information criterion (AIC) approach to minimizing models (Richards, 2008), whereby all models $\leq \Delta 6$ AIC are inspected, and the most parsimonious models with the lowest ΔAIC are retained, rejecting models that represent more complex versions of simpler nested counterpart models with lower delta AIC scores. Zero-one inflated beta binomial regressions were conducted using the GAMLSS package (Rigby and Stasinopoulos, 2001) in R 2.15.3 (R Development Core Team, 2011).

3.3. RESULTS

3.3.1. DESCRIPTIVE RESULTS OF FOCAL ANALYSES

The total number of focal observations recorded in the HA and IB was 469 and 550, respectively (Figure 3.3). All behaviours were present in the focal observations. On average, deer were observed to spend the most time engaged in resting behaviours in both the HA and the IB (mean proportional times = 0.614±0.02 and 0.497±0.02, respectively), whilst running accounted for the least displayed behaviour in both the HA and the IB (mean proportional times = 0.002±0.001 and 0.003±0.001, respectively). During the day period, deer were observed to spend the most time engaged in foraging behaviours in both the HA and the IB (mean proportional times = 0.485±0.034 and 0.437±0.04, respectively), whilst running accounted for the least displayed behaviour in both the HA and the IB (mean proportional times = 0.001±0.001 and 0.004±0.002, respectively). During the night period, deer were observed to spend the most time engaged in resting behaviours during for both the HA and the IB (mean proportional times =

0.739±0.024 and 0.526±0.024, respectively), whilst running accounted for the least displayed behaviour in both the HA and the IB (mean proportional times = 0.004±0.002 and 0.003±0.001, respectively).

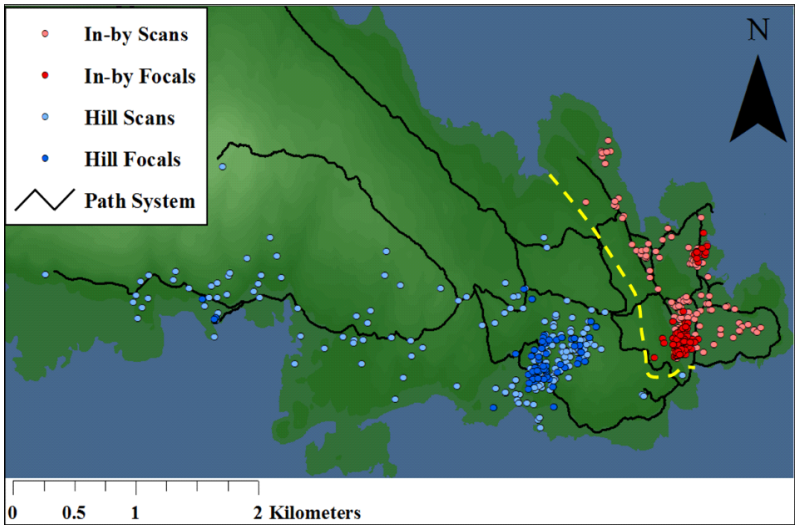


Figure 3.3. Positions of the total observations recorded on red deer herds (n=1157) throughout the study, differentiated into HA (blue) and in-by (red). Scans which were paired with counterpart focal observations (n=1019) are delineated by darker shades of respective site colour. Positions will denote multiple data points when herd positions remain stationary between scan sampling intervals. Deer fence separating IB and HA is represented by yellow dotted line.

Herd size was on average larger in the IB than in the HA (Table 3.2), but the largest herd size recorded was in the HA with 23 individuals, compared to 16 individuals for the IB. Recorded deer positions in the HA ranged in altitude from 2.166mamsl to 290.6mamsl. The lowest and highest altitudes of deer positions recorded in the IB were 0m and 71.38m, respectively. Including unsurfaced paths, the shortest and longest distance from a deer position to the nearest path recorded in the HA was 0m and 350m, respectively, with an average distance to the path of 85.911±4.198m (Table 3.2). Excluding unsurfaced paths, the shortest and longest distance to the nearest path recorded in the HA was 0m and 936.4m, respectively, with an average distance to the path of 407.3±7.918m. In the IB, the shortest and longest distance from a deer position to the nearest path recorded was 0m and 269.1m, respectively, with an average distance to the path of 61.071±1.712.

Table 3.2. Means of non-categorical predictor variables recorded at each focal (±SE), calculated for both HA and IB sites during the day period (HAD, IBD, respectively) and twilight period (HAN, IBN, respectively) and for both light periods combined (HA, IB). Mean figures are averaged across the total number of scans (N) respective to the appropriate site and light period combination. Wind speed is given in km/s; temperature is given in ° C; path distance and altitude are given in m; aspect is given in decimal degrees and slope is given in degrees.

Predictor	HAD (N=165)	HAN (N=304)	HA (N=469)	IBD (N=101)	IBN (N=449)	IB (N=550)
Herd size	8.267 (0.396)	5.503 (0.14)	6.475 (0.177)	5.545 (0.325)	7.886 (0.201)	7.456 (0.179)
Wind speed	4.275 (0.409)	1.184 (0.108)	2.271 (0.174)	1.463 (0.119)	1.138 (0.064)	1.198 (0.057)
Temperature	11.339 (0.359)	10.251 (0.164)	10.634 (0.167)	13.876 (0.164)	13.121 (0.135)	13.26 (0.115)
Path distance	117.81 (8.81)	68.597 (4.047)	85.911 (4.198)	83.856 (4.412)	55.946 (1.762)	61.071 (1.712)
Altitude	53.144 (2.414)	40.324 (2.286)	44.834 (1.73)	12.239 (0.302)	11.258 (0.19)	11.438 (0.166)
Aspect	234.763 (7.288)	210.307 (5.227)	218.911 (4.278)	131.841 (6.914)	208.47 (3.532)	194.398 (3.393)
Slope	8.675 (0.509)	5.145 (0.199)	6.387 (0.234)	7.349 (0.609)	3.943 (0.228)	4.569 (0.224)

3.3.2. DIFFERENCES BETWEEN PATH TYPE IN THE HILL AREA

The retained predictors for the PATH1, PATH2, full HA model and the IB for each of the behavioural responses investigated are presented in Table 3.3. Including surfaced paths within the path system affected which predictor variables and associated interaction terms were retained in the final model. For all analyses, nychthemeral period, sex, herd size, rain, wind, temperature, age class, weekday/weekend, and slope were not retained in the final models for any of the behaviours analysed.

3.3.3. INVESTIGATING THE EFFECTS OF ALL PATHS IN THE HILL AREA: PATH1

Regarding foraging behaviours, deer responded to path proximity similarly for both seasons. The proportion of time spent foraging did not change with increasing distance from the path until approximately 100m, after which a negative relationship was exhibited, and overall foraging was significantly lower in tourist season than non-tourist season (Figure 3.4, Table 3.3). The amount of time engaged in head-raised behaviours was not affected by path proximity in the non-tourist season, but was significantly higher with increasing distance to the path in tourist season (Figure 3.4, Table 3.3).

Table 3.3. The best zero-one inflated beta regression models within 6 ΔAIC, ignoring more complicated model counterparts with higher ΔAIC (Richards, 2008), whilst considering: all paths in the HA (PATH1); paved-paths only in the HA (PATH2); with habitat effects in the HA (HAB HA), and all effects recorded in the IB. Degrees of freedom are denoted by '*df*'. Coefficients for precision parameters ν and τ are given where 0 and/or 1 values are present, respectively. Coefficient standard errors are given in parentheses.

Model		***df***	**ν**	**τ**	AIC_c	R_2
PATH1 HA models (all paths)						
Behaviour	**Retained variables**					
Foraging	SEASON:PD	14	0.003 (0.001)	-	308.021	0.211
Ruminating	SEASON	5	-	-	239.022	0.111
Head-Up	SEASON:PD	11	-	-	318/067	0.141
Alert	PD	5	-	-	153.457	0.141
PATH2 HA models (surfaced paths only)						
Behaviour	**Retained variables**					
Foraging	PD + PT + SEASON	10	-0.002 (0.001)	0.070 (0.031)	316.861	0.163
Head-up	PD:PT + SEASON	8	-	-	238.891	0.129
HAB HA (all remaining variables)						
Behaviour	**Retained variables**					
Foraging	DN + HAB_G + HAB_{HM}	11	1.511 (0.238)	2.827 (2.058)	441.21	0.210
Ruminating	HAB_G + HAB_{HM}	7	1.121 ((0.215)	-	310.405	0.101
Head-Up	HAB_G + HAB_{HM}	7	0.002 (0.001)	-	445.473	0.142
Active	HAB_G + HAB_{HM}	7	1.731 (0.250)	-	39.522	0.161
IB (all variables)						
Behaviour	**Retained variables**					
Foraging	DN + PD	7	1.210 (0.253)	-1.241 (1.688)	611.457	0.109
Ruminating	SEASON:PT	6	1.053 (0.288)	-	310.139	0.151
Head-up	DN:PD + PT:PD + PV	10	1.408 (0.323)	-	517.241	0.125

† PD, PT and PV represent Distance to the nearest path (m), Traffic level of the nearest path, and Visibility of the nearest path. DN is Day/Night cycle. HAB represents Habitat, whereby categories 'G' and 'HM' represent Grass and Heather-mosaic. HAB HA represents the modelling of the HABITAT variable with mutual exclusion to PV, PT and any interaction effects between PD, PT, PV and SEASON. A '-' in the ν or τ denotes the absence of zero and one values, respectively.

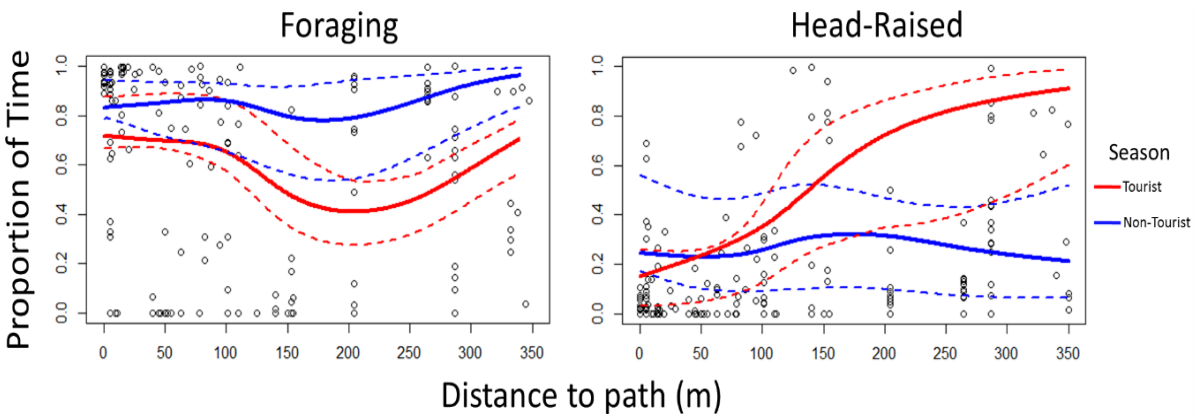


Figure 3.4. Interactive effect of season with the distance to the nearest path acting upon foraging (left) and head-up (right) behaviours recorded in the HA. Solid line represents the mean main prediction calculated from 1000 bootstraps whilst holding all other variables retained in the model at respective means. The area between the dotted lines of a given colour represents 95% CIs. Points represent jittered observations. The traffic of way-marked trails are considered (PATH1).

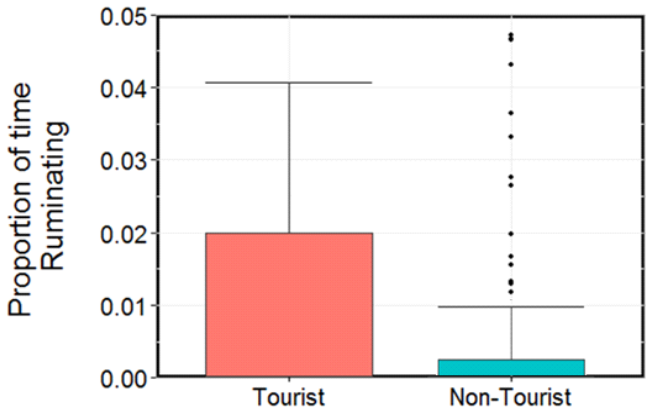


Figure 3.5. Main effect of season on the proportion of time engaged in ruminating behaviours in the HA. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outliers. The presence of unsurfaced paths is considered (PATH1).

Deer spent significantly more time engaged in ruminating behaviours during the tourist season than the non-tourist season (Figure 3.5, Table 3.3). Path proximity affected the amount of time engaged in alert behaviour (Table 3.3). Specifically, deer spent significantly more time engaged in alert behaviours as distance to the nearest path increased (Figure 3.6).

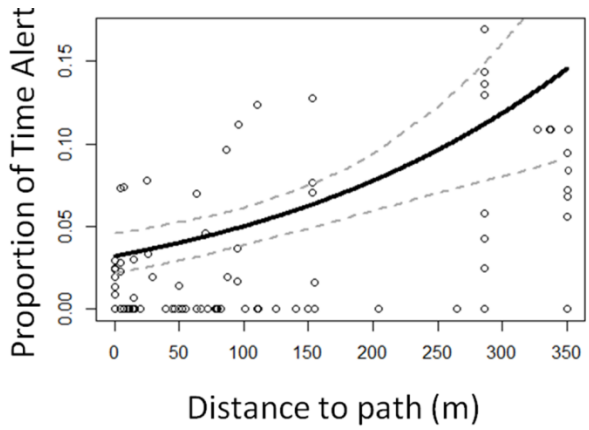


Figure 3.6. Effect of distance to the nearest path on foraging (left) and head-raised (right) behaviours recorded in the HA. Solid line represents the mean main prediction of the variable of interest whilst restricting all other predictors retained in the best model at mean values. Dotted lines represent confidences intervals (CIs) calculated from bootstrapping the respective main prediction (n=1000). Data points are jittered to show overlapping values.

3.3.4 DISREGARDING UNSURFACED PATHS IN THE HILL: PATH2

No variables explained either alert or ruminating models in the PATH2 analysis (Table 3.3). Foraging and head-raised behaviours were both significantly affected by the season (Table 3.3). Deer spent more time foraging in the non-tourist season, and more time engaged in head-raised behaviours during tourist season (Figure 3.7). Head-raised behaviours were also affected by an interaction of path proximity with path traffic (Table 3.3). When the nearest path experienced low traffic, the proportion of time engaged in head-raised behaviours did not change with path proximity (Figure 3.8). However, when the nearest path experienced high traffic, the head-raised behaviours increased in a linear fashion with increasing distance to the nearest path.

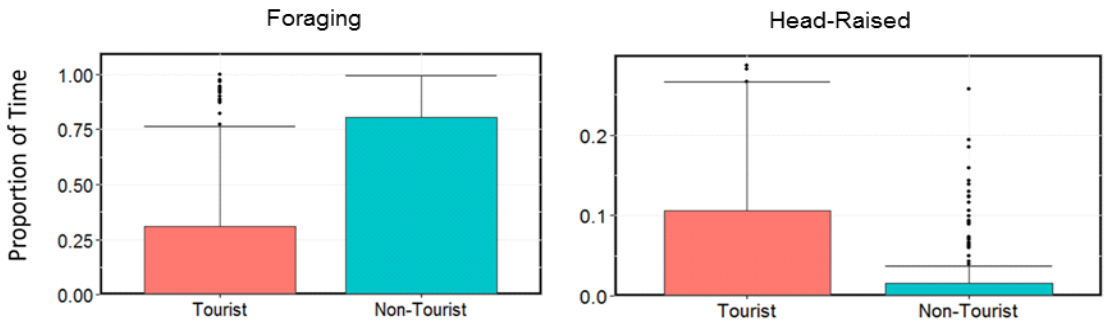


Figure 3.7. Main effect of season on the proportion of time engaged in foraging (left) and head-raised (right) behaviours in the HA. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outliers. Unsurfaced paths are excluded in the analysis (PATH2).

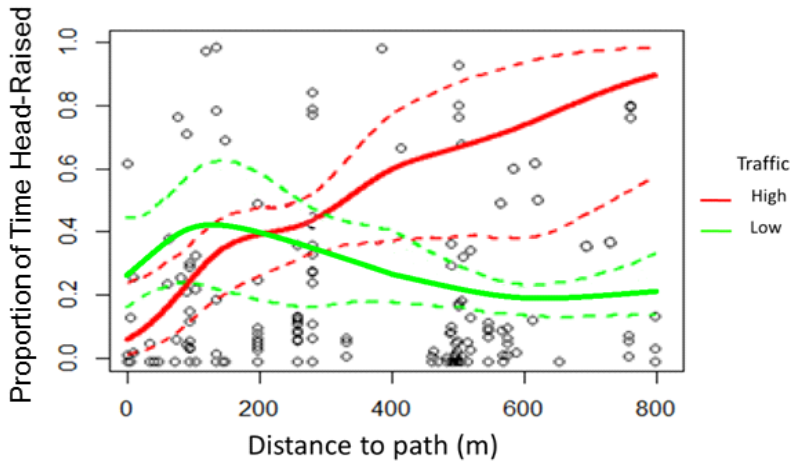


Figure 3.8. Interactive effect of path traffic with the distance to the nearest path acting upon the proportion of time engaged in head-raised behaviours recorded in the HA. Solid line represents the mean main prediction of the variable of interest whilst restricting all other predictors retained in the best model at mean values. Dotted lines represent confidences intervals (CIs) calculated from bootstrapping the respective main prediction (n=1000). Data points are jittered to show overlapping values.

Path proximity was found to affect foraging times, in which time spent foraging increased slightly with increasing distance; however this appears to be a weak effect (Figure 3.9, Table 3.3). Foraging was also affected by path traffic (Table 3.3), whereby deer spent significantly more time engaged in foraging behaviour when the nearest path experienced low traffic compared to when the nearest path experienced high traffic (see Figure 3.10).

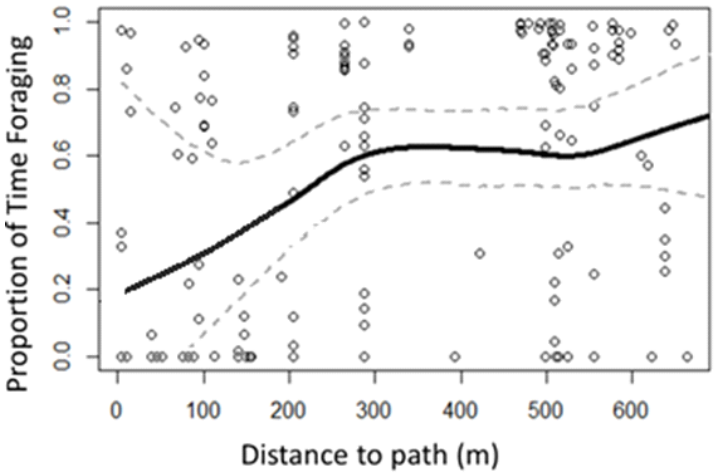


Figure 3.9. Main effects of distance to the nearest path acting upon the proportion of time engaged in foraging behaviour recorded in the HA. Solid line represents the mean main prediction of the variable of interest whilst restricting all other predictors retained in the best model at mean values. Dotted lines represent confidences intervals (CIs) calculated from bootstrapping the respective main prediction (n=1000). Data points are jittered to show overlapping values.

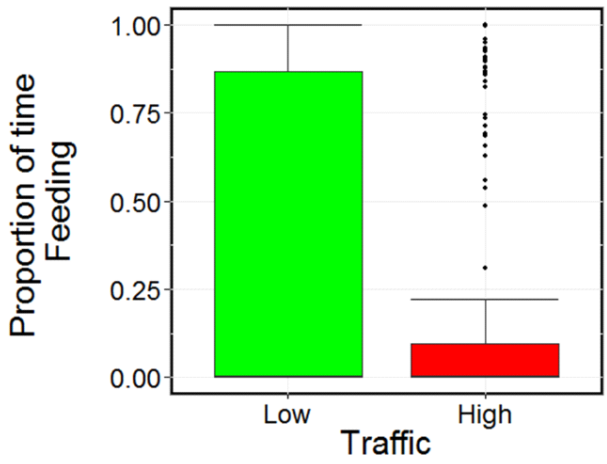


Figure 3.10. Main effect of traffic of the nearest path on the proportion of time engaged in foraging behaviour in the HA. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outliers. The traffic of unsurfaced paths is excluded (PATH2).

3.3.5. HABITAT EFFECTS ON DEER BEHAVIOUR IN THE HILL

Deer behaviours were recorded in bracken-mosaic, bog, heather-mosaic and grassland habitats (Table 3.4), Deer spent significantly more time foraging, ruminating and in head-raised displays whilst occupying heather-mosaic and grassland habitats than in bog and bracken-mosaic habitats (Figure 3.11, Table 3.4). Deer spent similar amounts of time whilst engaged in resting, active and locomotion behaviours in all habitat categories (Table 3.4). Model convergence failed for the alert model.

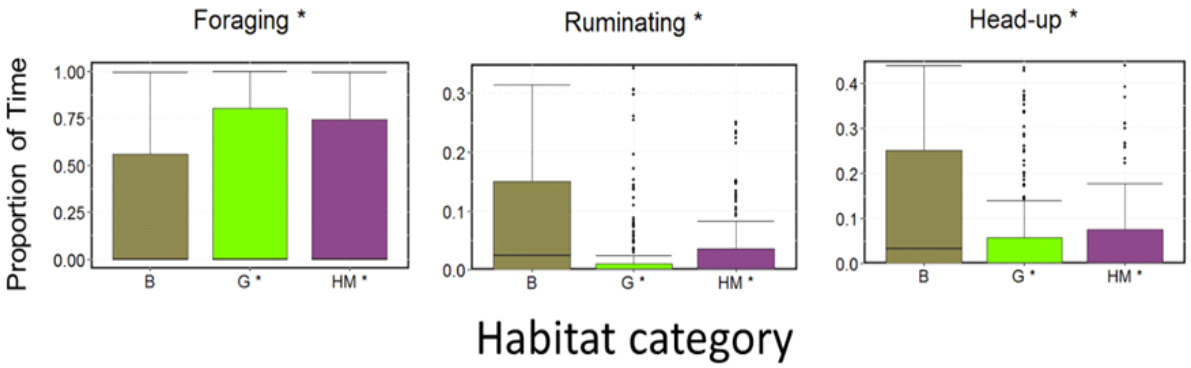


Figure 3.11. Proportions of time spent in each activity respective to habitat type in the HA: Bog (B); Grassland (G) and Heather-Mosaic (HM). Response models in which habitat was retained as a predictor are presented in the top row (denoted by an '*'), showing a significant change in G and HM from B (non-significant BM was excluded).

Table 3.4. All activity budgets for red deer for HA sites recorded on pooled habitat group 'Bracken-Mosaic' (BM), grass (G), bog (B) and pooled habitat group 'Heather-Mosaic' (HM). Figures listed are the mean percentage times spent in a given behaviour (±SE) averaged across the total number of focals (N) respective to the appropriate habitat category.

Behaviour	BM (N=16)	G (N=261)	B (N=42)	HM (N=149)
Foraging	0.175 (0.094)	0.296 (0.026)	0.255 (0.057)	0.296 (0.033)
Rest	0.748 (0.11)	0.627 (0.029)	0.515 (0.073)	0.609 (0.039)
Walking	0.001 (0.001)	0.026 (0.005)	0.036 (0.013)	0.035 (0.009)
Ruminating	0.017 (0.011)	0.036 (0.007)	0.146 (0.037)	0.035 (0.006)
Alert	0.002 (0.002)	0.007 (0.002)	0.028 (0.018)	0.017 (0.006)
Running	0 (0)	0.001 (0)	0.008 (0.005)	0.001 (0.001)
Head up [a]	0.02 (0.011)	0.071 (0.01)	0.219 (0.048)	0.089 (0.016)
Active [b]	0.195 (0.1)	0.367 (0.029)	0.473 (0.072)	0.385 (0.039)
Locomotion [c]	0.001 (0.001)	0.027 (0.005)	0.045 (0.017)	0.037 (0.009)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running; [c] Locomotion = Walking + Running

3.3.6. NYCHTHEMERAL EFFECTS ON INDIVIDUAL DEER BEHAVIOUR IN THE HILL

In the HA, deer foraging peaks at least once throughout the 24hr cycle, coinciding with the onset of the night period. A small decline in in foraging is seen directly at sunset, but this effect is debatable on the basis of wide confidence intervals. Foraging declines in the first half of daylight, the second half of night, and to a lesser extent at sunset. No other behaviour was related to the nychthemeral cycle (Figure 3.12, Table 3.5).

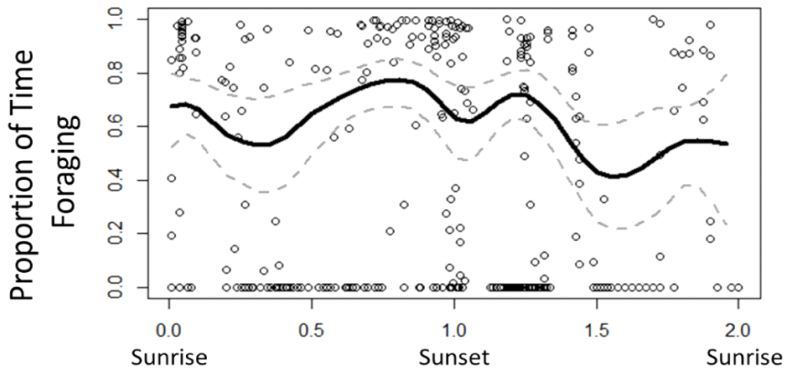


Figure 3.12. Main effects of the 24hr-cycle acting upon the proportion of time engaged in foraging behaviour recorded in the HA (full dataset). Solid line represents the main prediction of the predictor of interest whilst holding all other variables retained in the model at respective means. CIs are calculated from 1000 bootstraps. Points represent jittered observations.

3.3.7. INVESTIGATING DEER BEHAVIOUR IN THE IN-BY

Regarding the IB analysis, alert, locomotion, active and ruminating behaviours were generally consistent between day and night (Figure 3.13, Table 3.6). Head-raised behaviours were affected by an interaction between the distance to the nearest path and the traffic of that path, specifically, that head-raised behaviours increased with increasing distance to high-traffic paths, whilst a negative trend was found the nearest path was of a low traffic category (Figure 3.13). Head-raised behaviours were also affected by an interaction of path proximity and the nychthemeral cycle. Specifically, there was no effect of distance to the nearest path on head-raised behaviours during the night period, whilst a negative effect was evident during the diurnal period (Figure 3.13). Visibility was also retained in the head-raised model as a main effect (Table 3.3), whereby deer spent slightly more time engaged in head-raised behaviours as path visibility increased (Figure 3.14).

Table 3.6. Activity budgets for red deer for both HA and IB sites calculated during the day period (HAD, IBD, respectively) and the twilight period (HAN, IBN, respectively). Figures listed are the mean percentage times spent in a given behaviour (±SE) averaged across the total number of focals (N) respective to the appropriate site and light period combination.

Behaviour	HAD (N=165)	HAN (N=304)	IBD (N=101)	IBN (N=449)
Foraging	0.485 (0.034)	0.184 (0.02)	0.437 (0.04)	0.351 (0.019)
Rest	0.383 (0.037)	0.739 (0.024)	0.369 (0.046)	0.526 (0.022)
Walking	0.032 (0.007)	0.027 (0.005)	0.052 (0.012)	0.033 (0.003)
Ruminating	0.061 (0.011)	0.036 (0.006)	0.092 (0.017)	0.066 (0.007)
Alert	0.02 (0.006)	0.008 (0.003)	0.035 (0.009)	0.015 (0.002)
Running	0.001 (0.001)	0.002 (0.001)	0.004 (0.002)	0.003 (0.001)
Head up [a]	0.114 (0.016)	0.073 (0.01)	0.182 (0.026)	0.116 (0.009)
Active [b]	0.6 (0.037)	0.257 (0.024)	0.622 (0.046)	0.468 (0.022)
Locomotion [c]	0.034 (0.007)	0.029 (0.005)	0.056 (0.013)	0.036 (0.004)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running; [c] Locomotion = Walking + Running

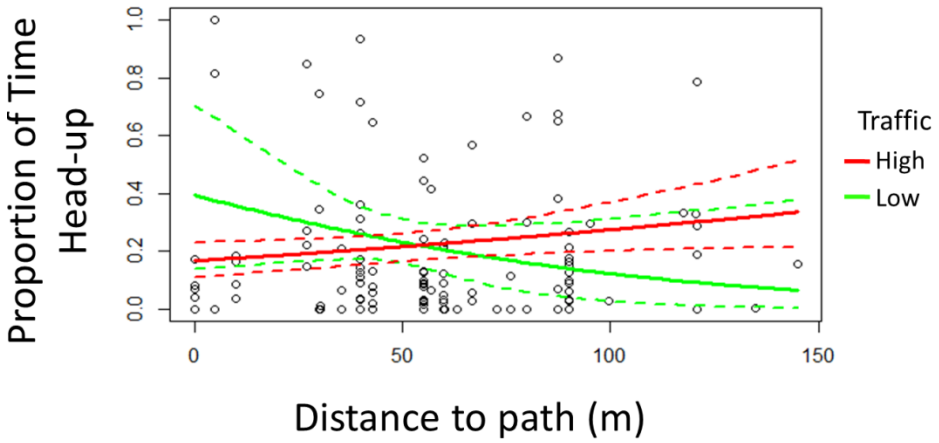


Figure 3.13. The interactive effect of path traffic with the distance to the nearest path (bottom), both acting upon the proportion of time engaged in head-raised behaviours recorded in the IB. Solid line represents the mean main prediction calculated from 1000 bootstraps whilst holding all other variables at respective means. The area between the dotted lines of a given colour represents 95% CIs. Points represent jittered observations.

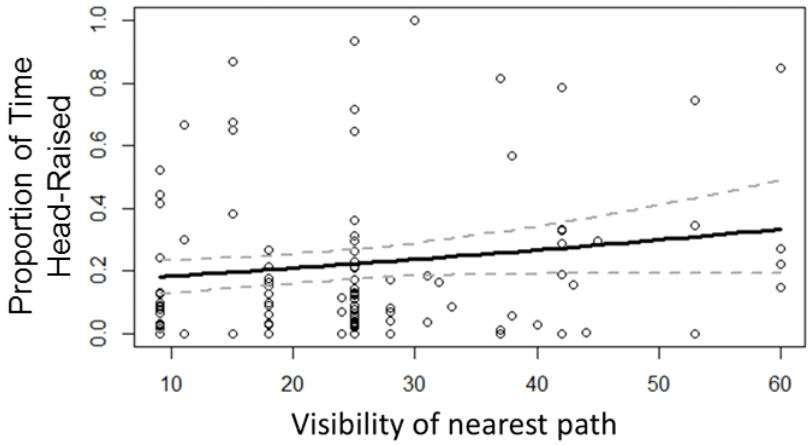


Figure 3.14. Main effects of path visibility acting upon head-raised behaviours recorded in the IB. Solid line represents the mean main prediction of the predictor of interest calculated from 1000 bootstraps whilst holding all other variables retained in the model at respective means. The area between the dotted lines represents 95% CIs. Points represent jittered observations.

For ruminating behaviours, an interactive effect of season and traffic category of the nearest path was found (Table 3.3). The proportion of time spent ruminating was similar between seasons when the nearest path experienced high traffic, but more time was spent ruminating during the tourist season when the nearest path was of a low traffic category (Figure 3.15).

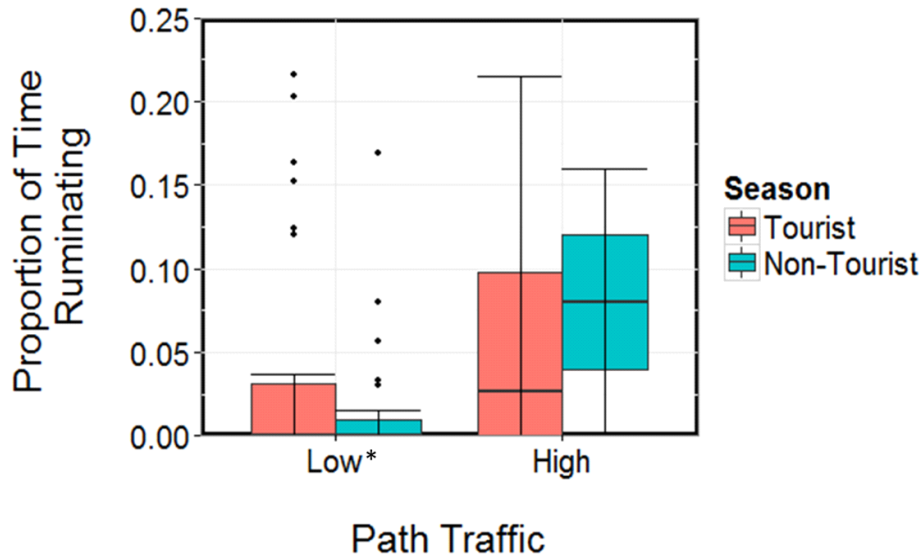


Figure 3.15. Interactive effect of season with the traffic of the nearest path acting upon ruminating behaviours recorded in the IB. Boxes represent the interquartile range from the median (solid line). Whiskers represent the 75th and 25th percentile, respectively. A significant interaction of season with path traffic category is indicated by '*'. Positions of potential outliers are denoted by points.

3.4. DISCUSSION

3.4.1. SUMMARY

The results of this chapter provided a comprehensive review of the behaviours exhibited by red deer throughout Ulva, and demonstrated the selection factors that described variability in behaviours. These behaviours observed in red deer are heavily context dependent, and varied dramatically with path type, season, site, and throughout the nychthemeral cycle. As the red deer of Ulva were hitherto unstudied, the results of this research provided the first collection of behavioural data for deer in this locality. Moreover, through the use of thermal imaging software, this study provided the first insight into deer behaviour throughout the nychthemeron.

The following is discussed: the effect of path systems and differences in response to surfaced and unsurfaced paths; modification of behaviours depending on the habitat occupied; the effects of seasonal change; the behavioural displays of deer throughout the nychthemeron; mention of environmental factors at play; and finally, the application of zero-one inflated beta binomial modelling is reviewed.

3.4.2. PATH SYSTEMS: A SOURCE OF DISTURBANCE

Foraging and head-raised behavioural responses to path proximity differed between seasons in the PATH1 analysis. Foraging slightly decreased as the distance to the path increased in both seasons, but was

significantly lower as a whole during the tourist season. On the other hand, there was no relationship between head-raised displays and distance to the path during the non-tourist season, but head-raised displays increased during the tourist season. Increasing foraging behaviours at the expense of vigilance behaviours as the distance to a source of disturbance decreases may at first glance seem counter-intuitive, but it was a recurring pattern throughout the current study: head-raised behaviours increase as distance to high-traffic paths increases in both the IB and the HA (PATH2); alert behaviours increase as distance to all paths increases in the HA, and foraging was shown to increase slightly with increasing proximity to surfaced paths in the HA.. The argument for these findings is based on the assumption that vigilance can be of two types, obvious head-raised vigilance, which increases scanning potential at the cost of foraging; and discrete head-down vigilance, whilst less effective, foraging is not interrupted (Lima and Bednekoff, 1999). Adding to this explanation, it was proposed that red deer will always opt for head-down vigilance when possible, and would resort to head-raised vigilance when potential sources of disturbance can no longer be sufficiently detected from head-down vigilance, or, a specific stimulus occurs, requiring head-raised vigilance for assessment. In the case of Ulva, the main source of disturbance was the path system (or specifically, the traffic use of the path). Deer could adequately scan the path at close distances whilst foraging, nullifying the need to express head-raised scanning behaviours. However, as distance to the path increases, deer were forced to increase head-raised vigilance in order to still scan the path, resulting in the consistent foraging and head-raised patterns observed. There was one caveat to this explanation: head-raised behaviours were found to increase as path visibility increased in the IB. According to the explanation at hand, head-raised behaviours should instead have increased to compensate for the loss of visibility of the path. However, the effect was weak, and was only present in the IB.

In the IB, ruminating behaviours increased in response to low-traffic paths during the tourist season. Perhaps the low-traffic paths represented a degree of unpredictability for the red deer as there was less regular traffic on these paths. Indeed, unpredictability associated with a disturbance has been shown to carry a greater effect (Sibbald et al., 2011a).

3.4.3. DIFFERENCES OF PATH STRUCTURE: SURFACED VERSUS UNSURFACED

Curiously, differing effects with respect to PATH1 or PATH2 analyses were found for a multitude of behaviours analysed at the individual scale. In the PATH2 analyses, head-raised behaviours increased

as distance to high traffic paths increased, but the effect was absent in the PATH1 analysis. Noting that all low-traffic paths were unsurfaced paths in the PATH1 analysis, this could be due to two distinct reasons, or a combination of both. Firstly, the simplest explanation is that the degree of tourist traffic on the unsurfaced paths was too low to elicit the same behavioural adjustments made in response to paths that experienced higher traffic. Secondly, it could be argued that, regardless of human activity, a difference in the response of deer behaviour towards unsurfaced paths and that of surfaced paths is in part due to the physical differences of the structures. Whilst both the surfaced paths and unsurfaced paths on Ulva disrupt the landscape by way of being unnatural, linear structures; paved paths were notably more conspicuous as ground flora was completely replaced by a surfaced component, which may in itself elicit a response in deer behaviour. Specifically, with such an obvious deviation in the natural landscape, surfaced paths could have been more easily detected than unsurfaced paths, and consequently, deer may have altered behaviour accordingly, whilst unsurfaced paths were not as readily noticed and so do not elicit the same behavioral adjustments (Nellemann et al., 2000b, Sibbald et al., 2011a).

Differences in the responses made with respect to unsurfaced paths and paved paths may be explained by another reason grounded on the differing physical characteristics of both structures, but additionally taking into account that deer associate the infrastructure with human presence. As surfaced paths were more conspicuous by design, then human use of paved-paths may have been easier to predict, as the flow of human traffic was dictated by the spatial dimensions of the path. As the boundaries of the unsurfaced paths were not easy to detect, deer were not provided with such obvious indicators of potential human activity as with surfaced paths. Indeed, Papouchis *et al*. (2001) found that familiarity of the nature of human disturbance is a key detail in explaining the degree of behavioural adjustments made by wildlife.

There are findings within this study that do not support the argument that deer behaviour is affected by the physical characteristics of paths alone. For instance, there were differences in response between low-traffic and high-traffic surfaced paths (same structure) and between surfaced and unsurfaced paths (different structures). This was evident in the PATH2 analyses, in which unsurfaced paths were completely removed and so both low and high traffic categories were represented by surfaced paths of a similar design. Here, it was found that deer did not alter the amount of head-raised behaviours expressed in response to paths that experienced low traffic regardless of the proximity of the deer to these paths, yet when the nearest path experienced high traffic, deer increased the amount of time spent in head-raised

behaviours as distance between the path and the deer position increased. This was also true of the IB, in which the distance to the nearest path only affected the time engaged in head-raised behaviours if the path experienced heavy tourist use. Therefore, it can be argued that the path systems were realised by the deer in terms of the traffic levels they experience, and whether the path was surfaced or unsurfaced may only minimally contribute to any path-related effects on behaviour. It was incidental that in this study the unsurfaced paths corresponded exclusively with low traffic levels. This is an important point, and conclusive statements regarding the effects of the physical nature imposed by surfaced and unsurfaced paths cannot be compared from the results of this study since it was not possible to compare path types of both forms that experienced similar degrees of tourist use. Taking into account that unsurfaced paths may have elicited stronger responses in wildlife due to the previously discussed familiarity effects (Sibbald et al., 2011a), these structures should be taken into consideration in other studies evaluating the impacts of path systems, but were herein ignored as path systems in discussing the results of this study. This decision was based on the following: whilst the two unsurfaced paths accounted for in the HA were extensive in size (**Chapter 2**), the traffic recorded upon each was minimal, and as such, the use of these unsurfaced paths was assumed to be analogous to infrequent off-path walking which was assumed to have occurred throughout Ulva over the course of the data collection periods (J. Howard pers. comms.).

3.4.4. HABITAT EFFECTS

Deer decreased the amount of time engaged in ruminating and head-raised behaviour when situated in grass and heather mosaic habitats, in favour of increasing time spent foraging. The explanation for these behavioural adjustments is twofold: firstly, whilst deer were known to forage to a certain extent on heather, grass habitats provided deer with more suitable forage in comparison to woody vegetation such as heather (Hofmann, 1989); and secondly, heather typically achieves a taller height than the habitats defined as grassland in this study, and as such, it incurred a visual obstruction for the deer at foraging heights. This meant that inconspicuous anti-predatory behaviours such as scanning the environment could not be achieved whilst engaged in foraging, and was performed with more obvious head-raised displays. Since head-raised behaviours mirrored the same pattern found with ruminating behaviours (Figure 3.9), which is itself a component of the head-raised category, it was likely that ruminating behaviours were the most frequent of the head-raised behaviours deer performed whilst in heather habitats. This supports the

suggestion that by increasing the time spent ruminating, deer were compensating for the visual obstructions whilst foraging in heather, as compared to other head-raised behaviours such as walking or running, ruminating was a more purposeful attempt to scan the environment (Lima and Bednekoff, 1999). This explanation is illustrated in Figure 3.16.

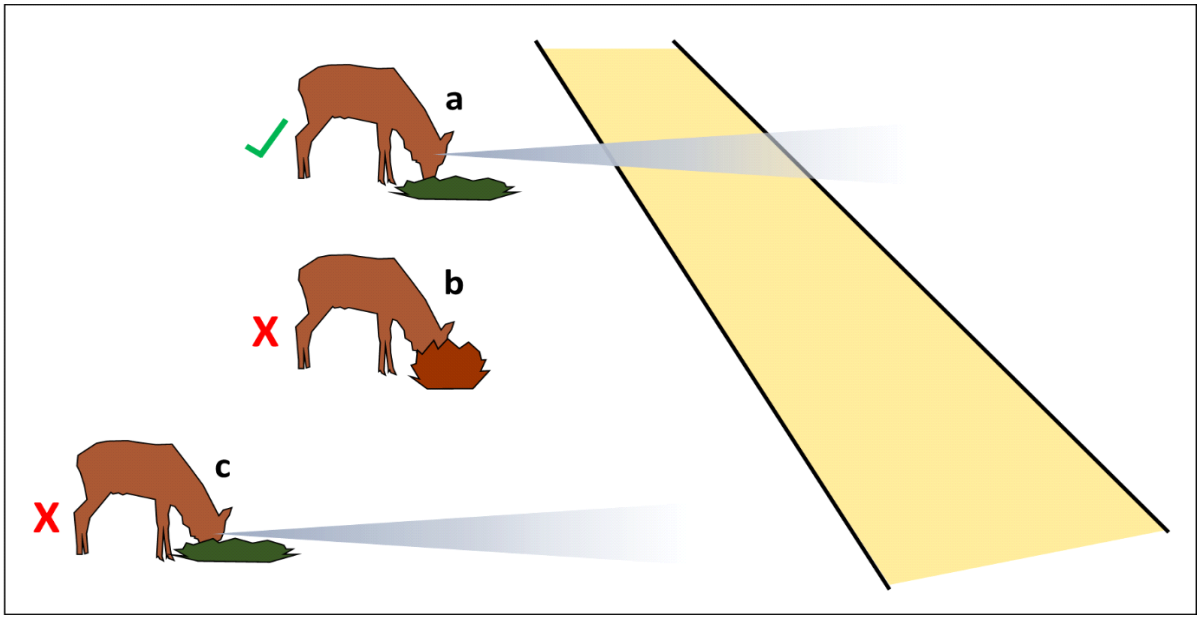


Figure 3.16. Schematic illustrating how behavioural adjustments are made in response to disruptions upon the passive scanning achieved whilst in the foraging position. The results of the current study show that deer foraged more in grassland habitats and with increasing proximity to paths, and engaged in head-raised behaviours more in heather mosaics and with increasing distance to paths. It is reasoned that head-down vigilance, as described in (Lima and Bednekoff, 1999), is sufficient in close proximity to the path, and head-raised vigilance behaviours are utilised when head-down vigilance is in some way disrupted. Here, the path is coloured yellow, deer 'a' and 'c' are foraging on grass, are able to view the landscape whilst foraging. However, deer 'c' is positioned unfavourably with regards to visualizing the path. Deer 'b' is foraging in heather, the height of which negates any scanning potential whilst foraging.

Alternatively, the locality of a majority of heather habitats on Ulva may have contributed to the observed behavioural adjustments in these sites. As described in Chapter 2, Ulva featured a general pattern of habitat change with increasing altitude, specifically with grassland habitats occurring at lower altitudes than heather-mosaics. This was particularly true on the south side where a majority of the focal samples were recorded. Therefore, deer positioned in heather mosaics would incidentally be at higher altitudes, and by scanning the environment via engaging in head-raised and ruminating behaviours would

benefit from the added vantage. However, alert behaviours decreased with increasing path visibility, and so if deer did increase anti-predatory behaviours in areas of good vantage, it was done so through passive monitoring (i.e. ruminating).

Jayakody *et al*. (2008) studied the relationship between vegetation heights associated with different habitats and anti-predatory behaviours in red deer, and in contrast to the study at hand, found red deer to exert more vigilance whilst lying down in grassland. It was suggested that the lack of vegetative height in grassland habitats exposed deer to potential sources of disturbance, and in response, deer lie down for cover when exhibiting vigilance (Jayakody *et al*., 2008). In the current study, there was no evidence that any potential cover provided by vegetation was found to be a factor in explaining behavioural patterns of red deer towards sources of human disturbance. Unlike the behavioural patterns observed in Jayakody *et al*. (2008), there was no relationship between resting behaviours and any habitat type. Therefore, the findings of this study did not support the idea that deer on Ulva may be appropriating certain habitats for general cover from detection of sources of disturbance.

Another possible reason for this apparent discrepancy between the two studies is due to differences in the observation protocol used. In this study, deer observed to be lying down were all classed as resting, whereas the study by Jayakody *et al*. (2008) differentiated lying down behaviours into 'non-vigilant lying down' and 'vigilant lying down', in which deer purposefully scanned the environment and exhibited twitching ear movements. This distinction would have not been appropriate for this study, since all resting deer were observed to exhibit similar head movements to the ruminating behaviour i.e. continuing mastication, relaxed ear positions, and therefore different levels of vigilance whilst resting could not have been identified. The populations of red deer studied on Ulva may exhibit entirely different types of behaviour from those studied in Jayakody *et al*. (2008) due to differences in hunting pressures. Jayakody *et al*. (2008) conducted observations in the Eastern Grampian Mountains in Scotland, which experiences an annual hunting season that lasts the entirety of autumn and winter. Whilst hunting does occur on Ulva, it is sporadic in its timing (generally taking place in September, January or February) and short-lived, usually occurring over the course of 1 week (J. Howard pers. comms.). It is plausible that deer which experience higher degrees of hunting pressures are forced to incorporate anti-predatory scanning

behaviours into other activities (Benhaiem *et al*., 2008), such as deer scanning the environment whilst resting, as observed in Jayakody *et al*. (2008).

Bog and bracken mosaic habitats did not significantly affect behaviour in any of the final models. Since bogs provided little in the way of forage and required relatively high levels of physical effort to traverse, there was little gain in occupying these habitats. Similarly, bracken habitats often represented the tallest vegetation on Ulva with the exception of woodlands, which potentially detered deer from using these habitats.

3.4.5. SEASONAL EFFECTS ON ULVA

Overall, a main effect of season was retained as a significant factor for multiple behaviours in the HA: an increase in foraging was observed during the non-tourist season; whilst head-raised and ruminating behaviours increased during the tourist season. As ruminating was a component of the head-raised category, it was plausible that a strong seasonal effect on ruminating behaviours was mirrored in the pooled head-raised category. An obvious explanation for the foraging and head-raised/ruminating patterns is that during tourist season, deer increase the amount of time in scanning the environment at the expense of foraging behaviours in response to the presence of hill-walkers (Borkowski, 2001, Cassirer *et al*., 1992, Fernández-Juricic and Schroeder, 2003, Jayakody *et al*., 2008).

It is important to note that the non-tourist season coincided with important annual events for red deer, namely the rutting season in autumn and the winter period, during which the availability of quality forage was decreased (Clutton-Brock *et al*., 1982, Godvik *et al*., 2009). This is a significant part of the annual cycle of red deer as notable changes in the body condition and physiology of red deer occur (Georgii and Schröder, 1983). Following the rutting season in late autumn, stags forage more to replace the energy lost from costly fighting and mating behaviours (Mitchell *et al*., 1976). Before the end of the non-tourist season, hinds carry new foetuses which incur energetic demands resulting in an increase in foraging behaviours (Georgii, 1981). Given the circumstances of tourist access on Ulva, it is difficult to tease apart the contributions of the intrinsic changes in deer physiology and behaviour and that of the tourist regimes in explaining the observed seasonal changes in activity budgets. It could be argued that the seasonal patterns of foraging observed in the current study would have occurred regardless of tourist presence. In comparing the behaviour of stags between sites with predators to the behaviour in predator-

free sites, Wolff and Horn (2003) found that whilst no difference in the amount of time engaged in vigilance behaviours occurred, the length of time engaged in foraging bouts was higher in the absence of potential predation. Moreover, Wolff and Horn's (2003) study was conducted specifically during the rutting season, during which stags are known to be particularly resilient to disturbance pressures (Bowyer, 1981, Clutton-Brock *et al*., 1982), and abruptly change from and to non-rutting activity budgets before and after rutting, respectively (Georgii and Schröder, 1983). Considering this, given that the rutting period was omitted from data collection during the non-tourist period, support is given in favour of disturbance pressures, or lack thereof, in contributing to the observed seasonal patterns. Indeed, even during non-tourist season, deer in the HA foraged less when the most proximate path experienced high traffic. Despite the lack of tourists at this time of year, deer may still have associated heavily-used paths with disturbance stimuli, and consequently refrained from engaging in long foraging bouts with high-use paths in the area as this would have made them susceptible to possible predation. Therefore, lag-effects of tourism may have altered foraging behaviours during the non-tourist season in the HA. Seasonal effects were not so prevalent in the IB; ruminating behaviours were the only behaviour affected by season, albeit, as part of an interaction. In the IB, deer ruminated more in the tourist season if the most proximate path featured low traffic. As discussed, unpredictable disturbances induced heightened responses in wildlife. Perhaps in the case of deer residing in the IB, passive scanning in the form of ruminating behaviours was adopted when near low-traffic paths, as path use was infrequent and therefore more unpredictable than in high-use paths. Unlike deer in the HA, deer reduced these passive scanning behaviours in the non-tourist season, suggesting that IB deer were more familiar with tourist presence throughout the seasons. Additionally, season did not affect the amount of time engaged in foraging behaviours for deer in the IB. Perhaps deer in the IB could tolerate human presence to such an extent that foraging bouts were not reduced during tourist season as humans were not seen as an important threat. This supports the argument that deer in the IB are more habituated to tourist presence than deer in the HA. Locomotion likely decreased during the non-tourist season in order to minimize energy expenditure both preceding and proceeding the energetically-intensive rutting period, and to overall conserve energy throughout the colder months (Craighead *et al*., 1973, Fancy and White, 1985). Additionally, hill-walkers present during the tourist season would have likely displaced deer. Detection of tourists on the path would have caused deer to migrate out of sight of the path, thus contributing to the increase in locomotion behaviours. Increased

locomotion in response to disturbance pressures is well documented (Frid and Dill, 2002, Stankowich, 2008), and human-related disturbances have been shown to increase locomotion behaviours in many ungulates, including red deer (Cassirer *et al*., 1992), mule deer (*Odocoileus hemionus*) (Freddy *et al*., 1986), guanacos (*Lama guanicoe*) (Donadio and Buskirk, 2006), mountain gazelle (*Gazella gazella*) (Manor *et al*., 2005), moose (*Alces alces*) (Andersen *et al*., 1996), bison (*Bos bison*) (Fortin and Andruskiw, 2003) and chamois (*Rupicapra rupicapra*) (Hamr, 1988).

It is not surprising that sex was not found to interact with season for the foraging or ruminating models, as previous studies have only revealed sex-specific differences with respect to these activities during the rutting season (Georgii and Schröder, 1983) due to extensive energy expenditures at this time (Moen, 1980), and the timing of fieldwork in the current study did not coincide exactly with the rutting season. However, sex-specific differences in the amount of locomotion has been shown to differ drastically proceeding the rutting period, whereby stags tend to move far less than hinds, presumably as behavioural adaptation for stags to address the lower body fat reserves left after the rut (Clutton-Brock *et al*., 1982, Pépin *et al*., 2009). The absence of this sex-specific difference in locomotory behaviours found in other studies may be due to the relatively easily traversed environment of Ulva (Pépin *et al*., 2006). It has been shown that strenuous activity during the winter incurs an energetic penalty upon deer that increases with respect to the degree of activity performed (Gates and Hudson, 1979). Consequently, deer may adjust the amount of time spent in locomotion according to the local environment, and indeed, deer that inhabit areas with little altitudinal variation and experience low snowfall have been shown to maintain similar levels of locomotion during the winter (Pépin *et al*., 2006, Pépin *et al*., 2009). Being an island, Ulva rarely experiences snow, and has a low altitudinal range of approximately 100m. Therefore, it is reasoned that despite the need to restore body reserves post-rut, stags on Ulva do not gain from spending less time in locomotory behaviours than hinds, and energy is returned via an increase in the foraging behaviours, as observed. Under this rationale, given that the IB features an abundance of improved grassland pastures and even less altitudinal variation, it is not surprising that seasonal effects on locomotory or active behaviours were absent in this site.

3.4.6. CHANGES IN ACTIVITY THROUGHOUT THE NYCHTHEMERON

Despite circadian rhythms being a topical area of research, studies that have investigated the diurnal activity patterns of wild animals has typically relied upon indirect methods of data collection such as radio-telemetry (Beier and McCullough, 1990, Georgii, 1981), or motion-sensitive accelerometers (Adrados et al., 2003, Moreau et al., 2009). The interpretation of data collected in this manner is arguably limited as information is recorded at a coarse scale and from small sample sizes (Pépin et al., 2006, Pépin et al., 2009), and/or enforcing invasive procedures of attaching and retrieving data recording equipment from specimens and thus incurring stress. To date, no studies have conducted 24 hour observations on wild free-ranging red deer, and therefore how sources of anthropogenic disturbance might be expressed on the 24-hour scale is unknown. The results of this chapter provide the first collection of direct behavioural observations conducted on free-roaming red deer throughout the entire nychthemeron, as well as demonstrating how certain behaviours change over the course of the 24hr cycle. Additionally, it reveals for the first time how behavioural adjustments made in response to path proximity change from day to night. As this is the first case of observing the diurnal and nocturnal patterns of free-roaming red deer, comparisons within the species can only be made with studies that conducted observations on captive red deer, or with studies that collected data remotely (e.g. GPS/radio collaring).

There was some evidence of compensatory foraging at twilight in the HA, and a crepuscular pattern of foraging was observed, as foraging peaked at both dawn and dusk. This was mirrored in the nocturnal period, with foraging bouts occurring after sunset and before dawn, and consequently deer exhibited a polycyclic pattern throughout the nychthemeron. Notably, there was a distinct lack of feeding synchronised with the timing of sunset. As these results reflect both seasons, the transition from light to dark clearly acts as an important zeitgeber for deer in the HA throughout the year. This apparent behavioural shift has hitherto not been observed. Without the day/night cycle being present in the final model for other behaviours, it is difficult to provide rationale for this observation. It should be noted that this trend could be a product of over-fitting the model on behalf of the smoothing parameter included for the day/night cycle variable. Indeed, the confidence intervals exhibit a poor fit to the main prediction with regards to this trend. It is plausible that the onset of the twilight period also signifies a change in observation techniques, as thermographic equipment is required to visualize deer in the dark, and this

apparent change in foraging signifies variation in recording techniques. This is unlikely, however, as given the distances from the observer to the deer in the HA, thermal imaging equipment was used much sooner than sunset in order to accurately observe the deer in the slowly dwindling daylight. Moreover, the behavioural categories recorded were analysed individually and as pooled categories, so the risk of misidentification for all behaviours is unlikely. Given that this trend occurs in the transition from day to night, it should not be overlooked in terms of biological rationale. It could be worth noting that although altitude was not included in the analyses (due to strong correlation with a main predictor of interest, distance to path), as twilight ensued, deer in the HA were observed to slowly move from higher altitudes towards the coastline, whilst slowly feeding. Acting as a zeitgeber, sunset could elicit a behavioural change in deer, which respond by migrating down-slope towards the coast. Navigating safely down the steep slope in increasingly dark conditions would necessitate locomotory and head-raised behaviours, causing a drop in the time spent foraging. If this were true, it is unclear why locomotory and/or head-raised behaviours did not peak at sunset.

A similar biphasic pattern with peaks of activity occuring at dusk and dawn instead has been revealed in previous red deer studies: in captive hinds (Pépin *et al*., 2006); stags in the Alps (Georgii and Schröder, 1983); in observations of herds in Germany (Bützler, 1974); and North America (Ward *et al*., 1976), and in many other ungulates, i.e. sambar deer (*Cervus unicolor*, (Semiadi et al., 1993), moose (*Alces alces*, (Cederlund, 1989), Iberian ibex (*Capra pyrenica*, (Alados, 1986), and roe deer (*Capreolus capreolus*, (Cederlund, 1989). However, the crepuscular patterns revealed in these studies were caused by peaks of 'activity', a broad behaviour informed from radio-collars in the case of Pépin *et al*. (2006) and Georgii and Schröder (1983), whereas the current study specifically shows a nychthemeral pattern of foraging behaviours, which may explain the previously undiscovered drop in foraging at sunset. Red deer exhibit strong behavioural plasticity towards environmental stimuli (Georgii and Schröder, 1983), and given that this foraging pattern was not observed in the IB, it may be in response to specific conditions inherent in the HA.

As previously mentioned, unlike deer in the HA, deer in the IB exhibit less anti-predatory behaviours in response to tourist season. This was proposed to be a product of habituation or tolerance to tourist presence in the IB, and may explain the difference in heightened feeding throughout the nychthemeral cycle between both sites. Deer may be engaging in longer foraging bouts at dawn and dusk

as these periods represent a lack of tourist activity and there is less risk of being disturbed. However, if deer show greater habituation towards human activity, then a tourist encounter is less likely to disrupt a foraging bout. This could be the case for deer in the IB, and as such there is no requirement to increase foraging during non-tourist times. In support of this, deer in the IB did not take advantage of the lack of tourist activity during non-tourist season and increase foraging times.

One caveat inherent in the methodology with respect to covering the day/night-cycle is a hide was required to conduct focal observations. The placement of which was limited to certain areas, which were determined by: the practicality of transporting and erecting a hide; suitable vantage; ease of access to the hide at all times including the night; and the likelihood of deer presence. This is very important, as deer strategically exploit spatial niches in relation to changing environmental conditions by adjusting activity patterns in favour of a given behaviour (Adrados et al., 2003b, Berger et al., 2002, Maier and White, 1998), but the use of environments in this capacity will also be temporally linked (Pépin *et al*., 2006, Pépin *et al*., 2009). Therefore, whilst the foregoing study presents ample data collected throughout the entire nychthemeron in both the IB and the HA, observations are nevertheless limited, as the 24hr cycle is represented by a subset of the total environment available to the deer. As such, a bias is introduced, and the behavioural patterns observed may be site-specific, which may explain the absence of temporal effects in many of the investigated behaviours. This issue may have been more prevalent when studying the IB, as extensive woodland reduced vantage and meant that observations were restricted to a given field. At a given time, the likelihood of encountering deer in given field differed, and consequently, the time of day was considered when choosing a field to observe. Since the IB is relatively uniform in terms of habitat variation, the predictability and constant proximity of human disturbance may be driving these patterns of field use throughout the 24hr cycle, rather than changing environmental conditions. Studies on activity patterns that collect behavioural data using activity counters embedded within radio-telemetry or GPS collars benefit from collecting continuous data from the animals, and so avoid any site-specific bias. However, these methods capture coarse measurements of behaviour, are typically restricted to small sample sizes, and miss short-term behaviours, focusing on broad behavioural categories as a result (Georgii, 1981, Georgii and Schröder, 1983, Pépin *et al*., 2009, Pépin *et al*., 2006). A system in which the terrain allows researchers to follow a target animal without inducing stress upon the animal, and with means to conduct direct observations via night vision or heat imaging technology would allow for fine-

scale observations of activity budgets throughout the nychthermeron. This is achieved for reindeer by Colman *et al*. (2001), although observer-elicited vigilance was likely a minimal issue, given that the focus was not on disturbance but rather feeding and resting patterns in response to biting insects during the summer, a time in which reindeer are more tolerant of human presence (Wolfe *et al*., 2000).

3.4.7. NOTES ON ENVIRONMENTAL AND GROUP SIZE FACTORS

Temperature, wind speed and the degree of rainfall did not affect deer behaviour. These variables were investigated as deer may have increased vigilance behaviours during fast wind speeds and heavy rainfall in order to overcome the lack of visibility and decreased ability to detect audio cues of sources of potential disturbance event due to adverse weather (Lingle and Wilson, 2001). There was no effect of weekday versus weekend on observed activity budgets. Deer have been found to maintain greater distances from path systems during days which routinely feature a lot of tourists (Sibbald et al., 2011a), but activity budgets may not be so adversely affected as habitat use. Indeed, a study of a population black-tailed godwits (*Limosa limosa*) found that whilst the birds avoided areas associated with tourists, the population did not suffer from a lack of foraging efforts (Gill *et al*., 2001a). Perhaps on Ulva, disturbance from walkers on Friday generates a lag effect that persists throughout the entirety of the weekend until walkers return on Monday. Overall, the herd size did not affect the response of deer to any of the path metrics, and very weak negative effects of herd size were found in both sites for foraging, and in the IB for resting behaviours. These results are somewhat incongruous with group size theories such as the risk dilution (Childress and Lung, 2003) and 'many eyes' hypotheses (Lima and Dill, 1990). For example, one would expect larger group sizes reduce predation risk for the individual through an accumulation of vigilant behaviours increasing predator detection potential leading to an increased perception of safety. As such, herding behaviour dultimately affords individuals time to engage in beneficial activities such as foraging and resting (Rieucau and Martin, 2008). However, these theories focus on vigilance activities, which were not affected by herd size in the current study, and so these results do not directly reject these hypotheses. In fact, herd analyses showed that IB deer were more likely to rest in larger herds, and at further distances from the path. These behaviours are not vigilance-related, and instead show a willingness to participate in vulnerable behaviours when in large groups, and at far distances from areas associated with tourist activity. Furthermore, factors such as sex, surrounding environment and browse preferences

are known to be more important in explaining individual vigilance/foraging budgets than herd size (Burger *et al*., 2000).

In the HA, foraging increased as the steepness of the terrain increased. Nubian Ibex (*Capra nubiana*) have been shown to increase foraging times when situated on slopes, as ibex are adept climbers, the terrain is perceived to act as a type of refuge from predation, and therefore less time is committed towards vigilance behaviours (Hochman and Kotler, 2007). Whilst red deer do not share the same relationship with steep terrain as members of the *Capra* genus, perhaps slope may still represent a degree of safety. Steepness of terrain did not show any collinearity with the habitat categories, so it is unlikely that deer are foraging more on slopes due to a relationship with a particular habitat, unless specific plants favoured by deer were found on slopes.

3.4.8. NOTES ON ZERO-ONE INFLATED BETA REGRESSION MODELLING

This chapter presents one of the first ecological studies to employ zero-one inflated beta regression modelling, as opposed to resorting to transformation procedures in order to meet modelling assumptions. Despite the prevalence of modelling continuous proportional data in behavioural and ecological studies, this approach has only been used twice, in a fishing report (Cañadas and Mhamed, 2016) and a brief report that exemplifies the use of zero-one inflated beta regression modelling on loggerhead sea turtle (*Caretta caretta*) data (Scott-Hayward *et al*., 2014). Whilst a high degree of model fit was achieved in most cases, the model failed to converge for certain behaviours. Since the alternative approach is to transform data in order to restrict the response variable between 0 and 1, convergence issues may not be an issue for this approach. Furthermore, zero-one inflated beta modelling is the more time-consuming and complex of the two methods, and so may not be appropriate for all analyses involving proportional data. However, there are disadvantages to transforming data (Ferrari and Cribari-Neto, 2004), and the appropriate approach undertaken for modelling proportional data will likely depend on the need for accurate model predictions versus the need for quickly processed results.

3.4.9. CONCLUDING REMARKS

It was expected that, in comparison to deer in the HA, the deer inhabiting the IB would exhibit behavioural patterns with respect to seasonal, nychthemeral, and anthropogenic disturbances that are

indicative of habituated deer. The results of this study offer evidence that in being subject to constant, proximate and high-level disturbance, deer in the IB exhibit activity patterns that suggest a strong degree of habituation has taken place. Support for this hypothesis stems from: differing responses to the 24hr cycle; fewer seasonal differences towards path systems in the IB; and stronger reactions to the path systems in the HA. The difference in behavioural patterns throughout the 24hr-cycle observed between the two sites can be explained by differences in respective disturbance regimes. Where frequent disturbance occurs, red deer have been shown to exhibit concentrated bouts of activity around dawn and dusk (Georgii, 1981, Hester *et al*., 1996, Pépin *et al*., 2006), as exemplified by deer in the HA. On the other hand, studies have shown that red deer inhabiting areas free of disturbance tend to exhibit activity throughout the entire day period, and utilise the nocturnal period for rest (Clutton-Brock *et al*., 1982, Pépin *et al*., 2006). Interestingly, this pattern is mirrored by deer in the IB. Habituation in ungulates does occur in response to heightened non-lethal disturbance, and is expressed by shorter flight distances and lowered vigilance rates (Picton, 1999). In the IB, not only is vigilance lower than in the neighboring HA population, but the fact that elements of the activity patterns mimic those of non-disturbed populations of red deer, suggests that disturbance in the IB is so constant as to cause extreme habituation to occur. It should be noted that these results only show habituation to increased non-lethal disturbance from a behavioural point of view (Stankowich, 2008), and potential malign effects from residing within the IB could be revealed through physiological investigations (Taylor and Knight, 2003).

Additionally, it is theorised that the consistent patterns emerging throughout the extensive analyses in this study show that deer will opt for head-down vigilance regardless of habituation, and are forced to display head-raised vigilance when the scanning potential achieved via head-down vigilance is in some way disrupted or a disturbance stimulus is encountered. This is likely due to the added benefit of being able to maintain foraging behaviours, with head-raised vigilance only outweighing continued foraging when head-down scanning potential can no longer manage risk assessment.

CHAPTER 4 SPATIAL RESPONSES OF RED DEER TO THE NETWORK OF PATHS AND TRAILS ON ULVA

'The wild deer wandering here and there,

Keeps the human soul from care'

- William Blake

4.1. INTRODUCTION

Human infrastructure has a profound effect on the environment, disrupting both the physical and chemical components, contributing to habitat loss, reducing the carrying capacity of the surrounding habitats, disrupting animal migratory patterns and modifying animal behaviour (Nellemann *et al*., 2001, Nellemann *et al*., 2003). There has been a substantial increase in infrastructure development in the last part of the 20th century (Nellemann *et al*., 2003), leading to extensive modifications of the natural landscape, such as the construction and maintenance of roads (Diamond, 1990, Noss and Cooperrider, 1994). This has prompted conservation ecologists to research how the ecological effects of road structures upon wildlife manifest (Trombulak and Frissell, 2000).

Anthropogenic disturbance has been repeatedly shown to reduce the extent wildlife use certain habitats by restricting animal movement or because areas such as paths or trails are associated with human traffic (Kaczensky *et al*., 2003, Malo *et al*., 2011, Pelletier, 2014). Nellemann *et al*. (2007) showed that bears can associate paths with high human activities, and this source of anthropogenic disturbance was sufficient to displace bear home ranges substantially. An important consideration of this effect is that wildlife may abandon high quality habitat in favour of less suitable habitats (Gander and Ingold, 1997). As wildlife responds to path use by avoidance, then depending on the volume of walkers and the density of the path systems, wildlife may in effect lose large portions of their habitat (Gander and Ingold, 1997). This effect of habitat loss can incur detrimental knock-on effects on the environment, and consequently, the displaced wildlife itself. For example, the redistribution of ungulates can lead to over-grazing on certain sites far from tourist activity, which in turn may result in reduced energy intake for individuals (Nellemann *et al*., 2001). On the other hand, evidence of habituation to path use exists in certain systems, whereby wildlife show little aversion to heavily-used paths, although this process is only thought to occur when the path-use is predictable and hikers do not leave the trails (Gander and Ingold, 1997). For example, Malo *et al*. (2011) showed that only a few areas in a tourist-frequented park were underused by guanacos (*Lama guanicoe*), and exhibited high tolerance towards human proximity with regards to flight initiation distance. The criterion for habitat selection in ungulates is the relative net energy available (Schmidt, 1993), and is influenced by a wide range of behavioural and environmental conditions (Adrados et al., 2003b), of which predator avoidance and forage availability are thought to be the most important (Schmidt, 1993). Certain

habitat types may not be beneficial to all of these criteria (Orians and Wittenberger, 1991), and trade-offs between the perceived costs and benefits are made when animals choose habitats (Lima and Dill, 1990).

For ungulates, a common trade-off occurs when the best forage is found in risky habitats, whilst terrain that minimizes predation risk provides poor forage (Godvik *et al*., 2009, Kauffman *et al*., 2007), and escape behaviour and refugia of choice alter depending on predatory behaviour. For example, Nubian ibex utilize steep cliffs as escape routes, and typically flee upslope when threatened (Hochman and Kotler, 2007), and steinbuck (*Raphicerus campestris*) respond to perceived predation by lying low in high vegetation (Riginos and Grace, 2008). Some ungulates rely upon early detection of predators and success of fleeing, such as the white-tailed deer, which actively selects open habitats (Lingle, 2002). Pelletier (2014) examined how trail-users in an ecotourism setting affect the habitat-use patterns of bighorn sheep (*Ovis canadensis*) and three cervid species: moose (*A. alces*), white-tailed deer (*Odocoileus_virgianus*) and elk (*C. elaphus canadensis*). For all species, high traffic reduced the use of areas that were visible from the paths, and furthermore, were more likely to occupy terrain that facilitated escape. Whilst red deer have been shown to perceive human non-lethal disturbance as a less acute threat than hunting (Jayakody *et al*., 2008), human-recreation disturbances are nevertheless mediated by spatial shifts and habitat selection (Wirsing *et al*., 2010). Furthermore, specific aspects of an animal's life history can dictate avoidance of infrastructure even when human presence is low or even absent (Nellemann et al., 2000a). For example, reindeer (*R. tarandus*) exhibit high sensitivity towards areas near paths during calving season, a time which features little human activity (Vistnes and Nellemann, 2001).

4.1.1. RESEARCH AIMS AND OBJECTIVES

In general, habitat selection in red deer is finely-tuned to even subtle changes in anthropogenic and seasonal pressures (which dictate forage availability, Schmidt, 1993). A well-documented method of estimating patterns of habitat use in ungulates is the pellet group count method (Hiirktinen, 1999), which provides reliable data under most field conditions (Neff, 1968). Indexing habitat use with pellet group count methods has been applied in moose, red deer, elk, roe deer, and bison (Acevedo *et al*., 2008, Acevedo *et al*., 2010, Kuijper *et al*., 2009, Lehmkuhl *et al*., 1994, Nellemann *et al*., 2001). Faecal pellet-group count methods can be divided into two categories: plot counts, where the sampling units are plots of a given size and location; and transect counts, where pellet counting operates within a strip transect (with a

fixed width throughout) or line transects (no fixed width) that employ distance sampling (Alves *et al*., 2013). Collins and Urness (1979) argued that faecal deposition differs between habitat types, and inferences upon habitat use should be evaluated with caution. The rates at which faecal pellets are deposited are related to the amount of time engaged in foraging behaviours, which is in turn affected by habitat type. For example, Loft and Kie (1988) found that pellet groups under-represented the extent of habitat use in conifer habitats, and conclude that this is due to deer utilizing conifer habitats for resting behaviours, but that it provides little forage. However, it has been argued that the rankings of habitat preference determined via pellet-group counts and direct observation methods yielded similar results, and so either method can be used to safely determine overall ranks of habitat use at a coarse scale, i.e. high-, medium-, and low-use habitats (Leopold *et al*., 1984). Indeed, Loft and Kie (1988) compared pellet-group count techniques with radio triangulation methods to assess habitat use in mule deer, and found that pellet-group counts were appropriate in ranking habitats by use, and concluded that the technique can provide useful information for wildlife management, albeit at a broad temporal scale.

The objectives of this chapter are twofold. First, in assuming that pellet presence is an index for habitat use, the first objective is to assess how levels of exposure to metrics of anthropogenic disturbance influence the habitat use patterns in red deer in both the HA and the IB, whilst considering the effects of habitat and terrain. The second objective is to investigate the temporal overlap of path use between red deer and tourists in both the HA and the IB, in order to identify if the disturbance regimes particular to each site inform the degree and timing of path use by red deer.

Objective 1: Whereas the IB features dense network of paths, regular anthropogenic disturbance, and is a small, enclosed area with many man-made barriers (e.g. housing, walling, fencing), the HA features comparatively infrequent disturbance, larger open spaces allowing for less exposure to sources of anthropogenic activity. Given that predator avoidance and forage availability are thought to be the main influences in habitat selection, habitat use in the winter is expected to be wholly a product of the latter, which is notably different between the IB and the HA. Whilst winter will introduce a lack of available forage for the deer in both sites (Clutton-Brock *et al*., 1982), deer residing in the IB will benefit from comparatively abundant forage via extensive pastures. It has been shown that food-supplemented populations of red deer exhibit stable and predictable winter ranges centred on the feeding stations (Schmidt, 1993). Whilst the deer on Ulva are not food supplemented, it is assumed that the additional

forage in the form of pastureland in the IB will result in similarly predicable winter ranges that do not deviate substantially from summer ranges. In contrast, annual changes in the vegetation in the HA will dictate more detectable behavioural adjustments.

As predator-avoidance is also a key determinant of habitat use, to which the assumption is made that human disturbance is analogous in this capacity, it is expected that the path networks will be an important factor in describing patterns of habitat use during the tourist season. However, this effect was expected to differ between the two sites. Results from Chapter 3 indicate that deer residing in the IB exhibit a strong degree of apparent habituation in the form of reduced vigilance behaviours towards tourist pressures, and the path systems may not displace deer here.

Objective 2: Linear structures such as public roads, fire access roads, paths and power-line rights-of-way are typically considered to be accountable for a loss in ecological health (Noss and Cooperrider, 1994), however the exact mechanisms by which wildlife is affected by these structures is complicated and varied in nature across taxa (Trombulak and Frissell, 2000). The linearity and access of road/path structures may provide roaming animals with easy travelling corridors through otherwise challenging terrain (Thurber *et al*., 1994).

Ungulates which exist in predator-free environments and which are tolerant to human disturbance pressures have been shown to use roads actively as a means to facilitate movement through an otherwise obstructed terrain. For example, Nellemann *et al*. (2001) showed that a Norwegian population of reindeer exposed to no predation exhibited a lack of anti-predatory behaviours by using open fire roads to traverse through the tundra. Camera traps collect a record of species presence along with the time of the photograph taken, and they have been applied in investigating the nychthemeral activity patterns of wildlife (Griffiths and Van Schaik, 1993). Several studies have applied camera traps in revealing overlapping patterns of activity between sympatric species (Linkie and Ridout, 2011, Ridout and Linkie, 2009). However, these studies are generally limited in considering the overlap of overall 'activity', and use this broad behaviour to make inferences regarding predation or competition (Wang and Macdonald, 2009). To date, no study has applied these same methods in investigating how specific behaviours or areas of habitat use may overlap temporally between species. In the current study, these methods will be applied in order to investigate the temporal overlap of path-use between red deer and tourists in both the IB and the HA. On Ulva, a majority of tourist access is dictated by the ferry crossing service, of which the first and

last crossings operate at 0900hrs and 1700hrs GMT, respectively. Therefore, it is expected that a majority of tourist path-use would occur within that timeframe and decrease strongly afterwards. In avoiding tourist presence, it is anticipated that in general, deer will be observed to use the paths outside of those hours. Specifically, given that deer are most active at dawn and dusk, deer path use will peak at both of these times. This pattern of overlap may vary between the HA and the IB. Given that the IB features many obstructions in the form of dry-stone walling, fencing and housing that are not present in the HA, and as such it is expected that red deer will exhibit a stronger degree of path use in the IB in order to bypass these barriers. However, given that the IB features comparatively frequent tourist-related disturbance, it is anticipated that the IB will feature less temporal overlap in path use between deer and tourists. On Ulva, red deer are not exposed to strong anthropogenic pressures in the winter (barring miscellaneous farming activities in the IB), as the tourist season ends in late September, and resumes in March. From this, it is expected that red deer will exhibit a stronger degree of path use in the non-tourist period than in the tourist period. To test this, the temporal overlap of path-use between tourists and red deer will be investigated by positioning camera traps along the path, which will record the time of tourist or deer presence on the path.

4.2. METHODS

4.2.1. CREATING THE STUDY SITE

In the HA, the study was performed along the entire southerly coastline of the HA, extending northwards to approximately 100m north of the main path running throughout the south-side of the island (Figure 4.1.). In keeping with the geographic distribution of behavioural observations (**Chapter 3**), eight pastures in the IB were studied (Figure 4.2.). Moreover, given that the unrepresented areas of the IB are wooded with complex undergrowth components, the rate of finding pellets would have likely been affected.

To randomly position the habitat plots, the study areas were first delineated by digitally drawing a polygon over each study area using ArcGIS 10.1, after which study plots were randomly positioned within these areas using the in-built ‘randomise point’ feature. 300 plots were created in the HA for each field season. In the IB, 55 plots were created for the first field season in effort to maintain an approximately equal density of plots as the HA (2.7 plots per ha). This was increased to 85 plots in subsequent field seasons, as the original number was deemed inappropriately low when divided among the 8 pastures.

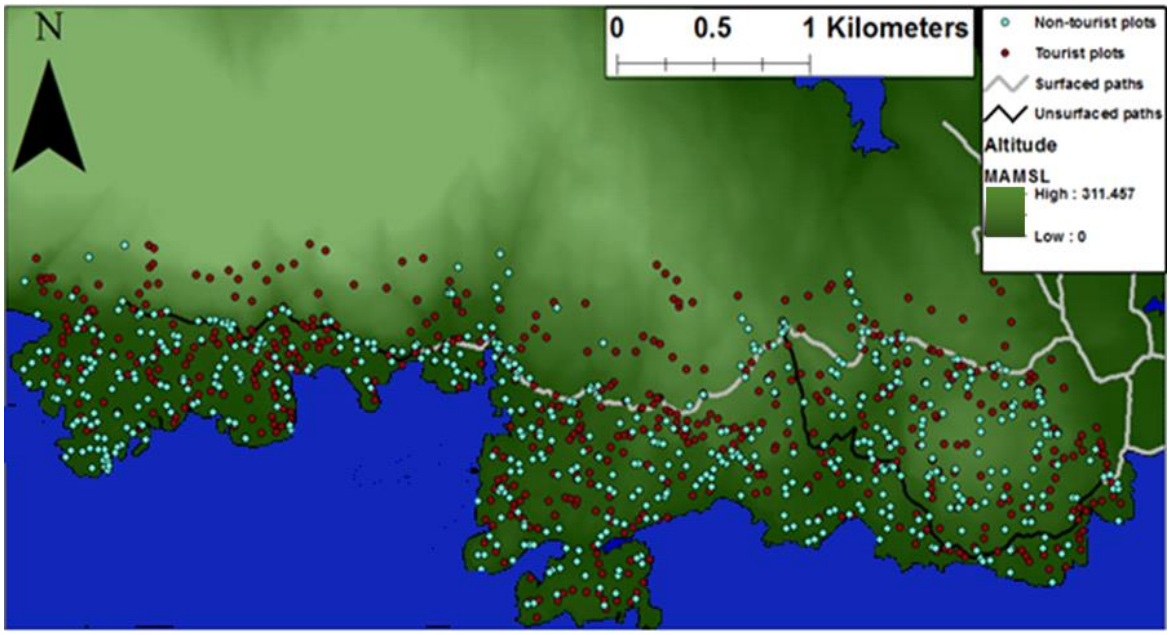


Figure 4.1. The positioning of all habitat plots in the HA study site in non-tourist (blue) and tourist (red) season. All plots were restricted to the south side of the HA.

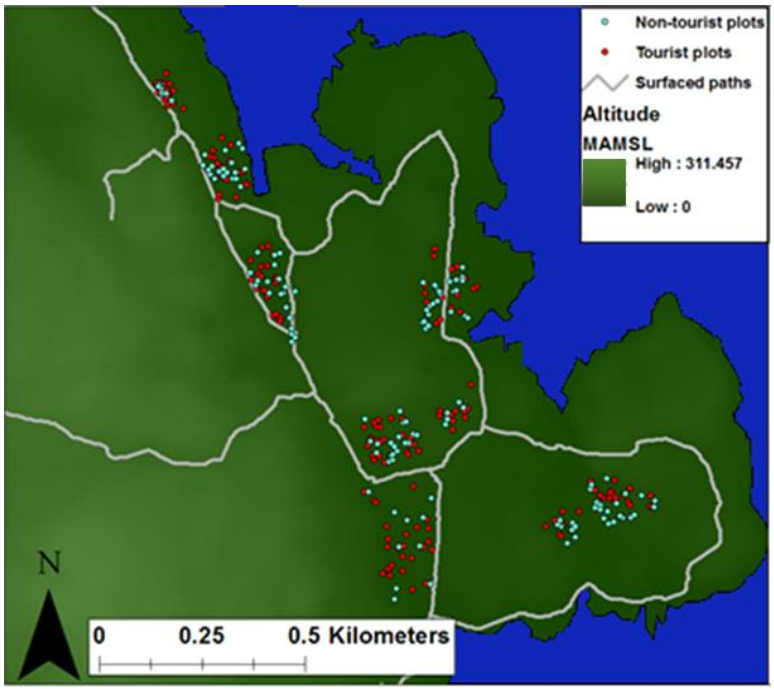


Figure 4.2. The positioning of all habitat plots in the IB study site in non-tourist (blue) and tourist (red) season. All plots were restricted to 8 pastures in the IB.

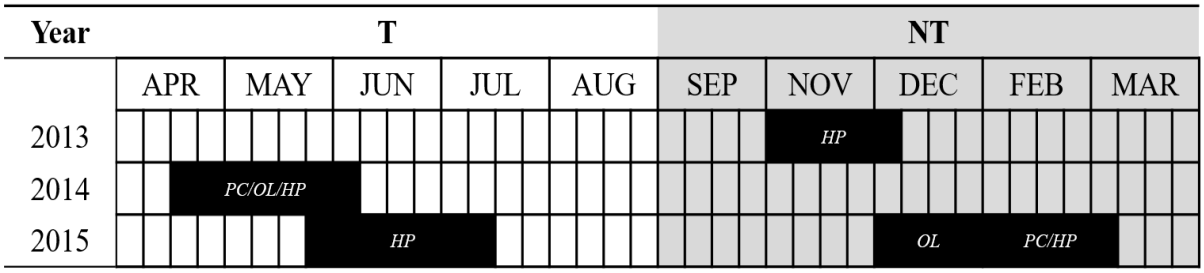
The plots were located by use of a Garmin eTrex GPS receiver, which directed the surveyors to the appropriate coordinates. Plots encompassed a 2-metre radius, delineated by a surveyor stranding at the plot coordinates and turning 360° with a 2-metre pole. For each plot, pellets were used as a proxy for

habitat use. The number of pellet groupings within the 2 metre radius was counted. Pellet groups were identified as a cluster of pellets. Singular pellets or sparse arrangements of pellets were ignored, as these may have originated from outside the plot, and have subsequently been moved by weather, sloping terrain or wildlife activity. Pellets pertaining to species other than red deer were also recorded to index habitat use by heterospecifics, such as greylag geese (*Anser anser*), domestic sheep (*Ovis aries*) and domestic cattle (*Bos taurus*). Deer trail presence was recorded as another index for deer habitat use. Habitat type (according to the criterion detailed in **Chapter 2**) was recorded at each plot.

4.2.2. TIMES AND DATES OF OBSERVATIONS

Habitat plots were recorded during both T and NT seasons from 2013 to 2015 (Table 4.1). Habitat plot recording was carried out at any time as long as there was ample daylight, as the identification of pellets was impractical at low levels of light.

Table 4.1. Time chart of fieldwork dates from 2013 to 2015. Each month is separated into 4 blocks, roughly corresponding to weeks. Months are arranged chronologically relative to season. Reading from left to right and from top to bottom, specific dates for habitat plots (*HP*) are 1 November 2013 to 1 December 2013 (NT); 20 April 2014 to 6 June 2014 (T); 1 February 2015 to 1 March 2015 (NT); and 24 May 2015 to 14 July 2015 (T). Plot clearing (*PC*) exercises were conducted once per season, specifically from 20 April 2014 to 11 May 2014 (T) and from 1 February 2015 to 22 February 2015 (NT). Temporal overlap of path use (*OL*) by deer and tourists was investigated once per season, specifically from 24 May 2015 to 14 July 2015 (T: 51 recording days) and from 29 November to 23 December 2015 (NT: 24 recording days).



4.2.3. PELLET RECORDING AND OBSERVER BIAS

Neff (1968) states that observer bias is a potential error source inherent in conducting pellet group counts and consequently, observer bias was accounted for in the current study. HO was the chief observer

for all field seasons. JD collected data simultaneously in November 2013, April 2014, February 2015 and May 2015. Observer bias was not considered a factor in the methods for two reasons. Firstly, as both observers collected data jointly for the first two field seasons, the recording protocol was standardised. Secondly, there was little room for error in counting the total amount of pellets per plot, as the only case that could potentially lead to a discrepancy between observer records would be when loosely arranged pellets are mistaken as a cluster, which was not encountered during data collection.

4.2.4. PLOT CLEARING EXERCISES

An important consideration when conducting pellet-group counts is the length of time pellets persist in the environment studied i.e. the decay rate (Alves *et al*., 2013), and inferences of habitat use in cervids can be confounded by variable rates of decomposition particular to different habitats (Neff, 1968). Collins and Urness (1979) argued that faecal deposition rates differ between habitat types and inferences upon habitat use should be evaluated with caution. The rate at which faecal pellets are deposited is related to the amount of time engaged in foraging behaviours, which is in turn affected by habitat type (Eberhardt and Van Etten, 1956). However, it has been argued that the rankings of habitat preference determined via pellet-group counts and direct observation methods yielded similar results, and so either method can be used to safely determine overall ranks of habitat use at a coarse scale, i.e. high, medium, and low-use habitats (Leopold *et al*., 1984). Indeed, Loft and Kie (1988) compared pellet-group count techniques with radio triangulation methods to assess habitat use in mule deer, and found that pellet-group counts were appropriate in ranking habitats by use, and concluded that the technique can provide useful information for wildlife management, albeit at a broad temporal scale. There are two methods in dealing with this issue, namely faecal standing crop, and faecal accumulation rate. With the former, decay rates are incorporated into a model in which the density of the species studied is a function between the numbers of pellet groups recorded with the average time that they remain in the study site. Secondly, faecal accumulation rates (FAR) involve clearing plots of pellets, which are returned to at a later date to record the number of pellets that have amassed (Mayle *et al*., 1999). Incorporating decay rate for standing crop counts requires a preliminary study to collect the decay rate specific to the species, season and area being studied (Campbell *et al*., 2004) and consequently, metrics of decay rates are often omitted from studies (Marques *et al*., 2001). Alves *et al*. (2013) compared the ability of the different methods in estimating a known density of

deer, and given that the FAR method requires plots to be visited twice, it is the more time-consuming and costly of the two methods, but yields accurate results where density of pellets and habitat heterogeneity exists. It is for these reasons that FAR methods were opted for in order to account for pellet persistence in the current study: the HA features strong habitat heterogeneity (grassland, bracken, heather mosaics). The FARs of pellets in both sites were investigated by conducting plot-clearing trials for each season. Habitat plots were separate from those investigated for habitat use and are herein referred to as Pellet Clearing (PC) plots. The methods for randomly placing PC plots were identical to those of habitat plots. In the HA, 50 plots were created for both T and NT plot clearing trials (total =100). Due to the lower number of replicates, habitat category recording at PC plots followed a more broad-scale approach than with habitat plots in order to acquire sufficient frequencies of habitats to allow for statistical analysis. To maintain consistency, the same criteria for pooling habitat categories when observing deer behaviour (**Chapter 3.2.7.1.**) were applied here.

4.2.5. MEASUREMENTS OF PATH-USE

Instances of path use by deer and tourists were recorded whilst simultaneously quantifying path traffic. Therefore, camera model specifications, the positions of the cameras in the HA and the IB and the camera rotation regime are detailed in **Chapter 2**. These aspects of the methodology were replicated when investigating path use during the non-tourist season. Multiple captures of distinct individuals were treated as separate data points. For example, if a photo taken at 1500 h showed two deer present, both individuals were included in the analysis (2 deer at 1500 h on the same date). Tourists present in subsequent photographs that were >15mins apart were treated as separate events and were included in the analysis.

4.2.6. STATISTICAL ANALYSES

4.2.6.1. HABITAT USE

A conservative approach was taken to analyse pellet counts in a dichotomous format (present/absent) to allow for a binomial regression of pellet presence. Similarly, with the **Chapter 3** analysis, HA and IB datasets were analysed separately. Predictor variables included the following path metrics (repeated for PATH1 and PATH2 systems): distance to the nearest path, traffic of the nearest path, visibility of the nearest path, season and all possible interaction combinations of these predictors. Other

predictors included habitat type, altitude, aspect, and slope. The degree of spatial-autocorrelation among habitat plots (pellet presence driving nearby pellet presence) was tested initially through the application of a Moran's autocorrelation coefficient. Moran's autocorrelation coefficient was performed using the 'Analysis of Phylogenetics and Evolution' (APE) package (Paradis *et al.*, 2004) in R version 2.15.3. Spatial-autocorrelation was accounted for in the model selection process by creating a spatial-autocorrelation variable (SAC) and including this as a predictor in the models. SAC was created in a two-step approach. 1) The pellet presence/absence values of habitat plots were interpolated for both sites separately using the 'Inverse-Distance-Weighted' interpolation tool (IDW) in ArcGIS 10.1. This created a surface raster (cell size = $5m^2$) that predicted pellet presence/absence of an unmeasured location from the measured pellet presence/absence values of the habitat plots surrounding the prediction location. IDW assumes that, for a given location, proximate habitat plots will have more influence on the predicted value than those more distantly located. In this study, habitat plots within a 50m radius of an unstudied location were considered for predicting a value. 2) As the IDW raster surface was calculated from the pellet presence/absence values of habitat plots, the values of the IDW cells in measured locations (directly underneath habitat plots) will represent the respective habitat plot pellet value. Therefore, to create the final SAC value, cell values underneath habitat plots were averaged from neighbouring values, by using the 'Focal Statistics' tool. SAC values for cells were formed by averaging all neighbouring cells within a 50m radius. This was the maximum area that herds were observed to occupy, and so the presence of pellets deposited by a red deer is likely to be spatially auto-correlated with a herd member less than 50m apart.

In order to test whether distance to the paths is a non-linear effect (i.e. paths may have a significant effect on habitat use close to the path, but not at far distances – which could hide the overall effect), pellet presence recorded in plots within a 10m buffer of the paths were tested against all other plots. In the HA, this process was repeated through 10m increments of the buffer radius, ultimately testing plots within a 100m buffer against all other plots. To express effect sizes, coefficients for retained continuous variables were converted into log odds, and the coefficients for categorical variables were converted into predicted probabilities (Hosmer Jr and Lemeshow, 2004). The final models were selected following the Akaike's information criterion (AIC) approach to minimizing models (Richards, 2008). All models $\leq \Delta 6$ AIC are inspected, retaining the most parsimonious models with the lowest ΔAIC values, in

addition to considering models that do not represent more complex versions of simpler nested counterpart models. Beta binomial regressions were modelled in R 2.15.3.

4.2.6.2. ANALYSING PATH OVERLAP BETWEEN DEER AND TOURISTS

To investigate the degree of temporal overlap in the patterns of path use by tourists and red deer, a similar method to Ridout and Linkie (2009) was used. Photographs were converted into a dataset that represented a random sample of a probability distribution that describes the probability of either tourists or deer being photographed at a given time throughout the nychthemeron. The probability density function of which is referred to as the path-use pattern, and assumes that the likelihood of photographing tourists or red deer using the path is constant at all times (Linkie and Ridout, 2011). The temporal overlap of path-use patterns between red deer and tourists were analysed for both inter-site differences (HA and IB) and intra-site differences (within HA). The HA is a large area that presents tourists with relatively long, linear path systems, as opposed to the circular routes in the IB. As such, it was considered that since a majority of tourists need to enter/exit the island via the ferry service operating in the IB, the temporal patterns of tourist path use will be heavily affected with respect to the distance to the IB. In turn, the HA may represent a variation in path-use by red deer. To investigate inter-site differences within the HA, the temporal overlap of path-use by red deer and tourists were analysed at both the east end of the HA path (camera position = HA2, see **Chapter 2**) and at the west end (camera position = HA5, see **Chapter 2**).

The coefficient of overlapping between deer and tourist activity was determined by following the method proposed by Ridout and Linkie (2009), whereby kernel density functions Δ_1 (when samples are at least $n > 75$) or Δ_4 (when samples $n < 75$) were fitted to the camera trap times for both deer and tourists. A quantitative measure ranging from 0 (no overlap) to 1 (complete overlap) was applied to the density functions to calculate the degree of overlap using the 'overlap' package (Meredith and Ridout, 2014) in R 2.15.3.

4.3. RESULTS

4.3.1. PLOT CLEARING EXERCISE

Total number of PC plots recorded for the HA was 206 (96 in T and 110 in NT; Table 4.2). Plot locations used in the pellet clearing exercise for the HA were evenly spaced and thus represented a

variation of habitats, altitudes and distances to the path systems. Habitat category frequencies are given in Table 4.2. The maximum and minimum altitudes recorded at PC plots in the HA were 0mamsl and 156mamsl, respectively. Considering both surfaced and un-surfaced paths in the HA (PATH1), the minimum and maximum distances to the nearest path in the HA were 0m and 602m, respectively. Clearing plots of pellets during the summer or winter did not affect the number of pellets found when revisiting the plots after a 3-week period ($\Delta AIC_{null} = 0$). FAR did not differ between habitat types ($\Delta AIC_{null} = 0$) nor with increasing altitude ($\Delta AIC_{null} = 0$). Finally, FAR was not significantly affected with increasing distance to the path ($\Delta AIC_{null} = 0$).

Table 4.2. Frequencies of broad-scale habitat categories recorded at PC plots during the tourist season and non-tourist season (definitions for broad-scale habitat categories are given in **Chapter 3.2.7.1**.).

Habitat type	Frequency T	Frequency NT
B	20	10
B^M	30	44
G^M	22	12
H^M	24	44

† ^{M} superscript denotes 'mosaic', and represents pooled habitat categories respective to the habitat type prefix.

4.3.2. DESCRIPTIVE RESULTS

The total number of habitat plots recorded in the HA and the IB were 1159 and 310, respectively (total=1329). The means (±SE) for altitude, aspect, slope, path distance and path visibility per season for both sites are given in Table 4.3. The minimum and maximum altitude of habitat plots in the HA were 0 and 207.226 mamsl, respectively, and in the IB were 4.041 and 21.637 mamsl, respectively. The minimum and maximum aspect of habitat plots in the HA were 0° and 359.511°, respectively, and in the IB were 4.041° and 21.637°, respectively. The minimum and maximum slope of habitat plots in the HA were 0° and 51.233°, respectively, and in the IB were 0.0717° and 32.989°, respectively. The minimum and maximum distances to the nearest path in the IB were 0.287m and 173.881m, respectively. Considering both surfaced and un-surfaced paths in the HA (PATH1), the minimum and maximum distances to the

nearest path in the HA were 0.007 and 1097.519m, respectively, and the minimum and maximum visibilities of the nearest path recorded were 0m and 587m, respectively (see **Chapter 2,** section **2.2.4.** for path visibility unit definition). When considering only surfaced paths in the HA (PATH2), the minimum and maximum distances to the nearest path in the HA were 0.024 and 2092.138m, respectively, and the minimum and maximum visibilities of the nearest path recorded were 0 and 302, respectively

Grassland represented the most frequently recorded habitat category for tourist season, and bracken represented the most frequently recorded habitat category for the non-tourist season (Table 4.3.). For both seasons, rocky outcrop was present in insufficiently low quantities to warrant statistical analysis, and was omitted from analysis due to statistical limitations. Rocky shore habitat category was omitted for similar reasons. With regards to the remaining habitats, moss-grass and grassy-bog were the least frequently recorded categories for the tourist season and non-tourist season, respectively.

Table 4.3. Frequencies of habitat categories recorded at habitat plots in the HA separated into data collection periods carried out in tourist season and non-tourist season (definitions for habitat codes are given in **Chapter 2,** section **2.2.6**.). RO and RS are removed from the dataset.

Habitat type	Frequency T	Frequency NT
B	69	157
Br	66	56
G	161	98
GB	60	30
H	52	36
HMG	124	129
MG	29	53

†Br represents pooled category 'Bracken-Mosaic' created from combining BG and BMG

Pellet presence/absence exhibited similar degrees of positive spatial-autocorrelation in both the HA (Moran's Index = 0.034±0.004, $P<0.001$) and the IB (Moran's Index = 0.029±0.011, $P<0.01$). Deer trail presence/absence exhibited weak yet significant positive spatial-autocorrelation in the HA (Moran's Index = 0.011±0.003, $P<0.01$) and to a stronger extent in the IB (Moran's Index = 0.051±0.011, $P<0.001$).

Table 4.4. Means of non-categorical predictor variables recorded at each habitat plot (±SE), calculated for both HA and IB sites during the tourist season and (HAT, IBT, respectively) and non-tourist season (HANT, IBNT, respectively) and for each site overall (HA, IB, respectively). Mean figures are averaged across the total number of habitat plots (N) respective to the appropriate site and season combination. Path distances is given in m, altitude is given in metres above maximum sea level, aspect is given in decimal degrees, slope is given in degrees and path visibility is expressed as the amount of path visible from the location of a given habitat plot (**Chapter 2,** section **2.2.4.**).

Predictor	**HAT** (N=574)	**HANT** (N=585)	**HA** (N=1159)	**IBT** (N=170)	**IBNT** (N=140)	**IB** (N=310)
Altitude	42.779 (1.626)	33.225 (1.198)	37.956 (1.016)	12.96 (0.332)	12.96 (0.38)	12.96 (0.25)
Aspect	172.322 (3.466)	179.148 (3.638)	175.768 (2.515)	135.957 (7.998)	151.148 (9.146)	142.818 (6.03)
Slope	11.69 (0.381)	10.721 (0.322)	11.201 (0.249)	4.883 (0.357)	5.778 (0.461)	5.288 (0.286)
PDIST[a]	233.787 (9.091)	259.323 (10.198)	246.676 (6.846)	58.733 (3.136)	61.249 (3.985)	59.869 (2.486)
PDIST[b]	657.338 (23.102)	611.042 (20.909)	634.41 (15.603)	-	-	-
VDIST[a]	86.181 (4.204)	90.026 (4.508)	88.122 (3.083)	59.512 (2.435)	63.679 (3.097)	61.394 (1.934)
VDIST[b]	42.866 (2.662)	44.67 (2.804)	43.77 (1.934)	-	-	-

[a] and [b] denote measurements calculated for PATH1 and PATH2 networks, respectively, and consequently PATH2 calculations are not reported for the IB site which only features surfaced paths.

4.3.3. HABITAT TYPE AND TOPOLOGICAL DETERMINANTS OF HABITAT USE

No interactive effect between predictors significantly influenced habitat use in the IB. Furthermore, the following variables did not significantly influence habitat use: aspect, path traffic, distance to the nearest path, and distance to the nearest woodland or the type of nearest woodland. Season and path visibility were retained in the best model ($\Delta AIC = 0$); however, a simpler model with featuring season as the sole predictor had a ΔAIC of 1.31, suggesting that season alone is an important driver of habitat use (Table 4.4). In both models, habitat use in the areas studied was significantly higher in the tourist season than non-tourist season, and path visibility shared a significantly negative relationship with habitat use (Figure 4.3; Table 4.4). In a given season, the odds of observing pellets in a plot decrease by 0.56% for every one-unit increase in path visibility. The predicted probability of observing pellet presence is 0.26 in non-tourist season and 0.41 in tourist season (Figure 4.3).

Table 4.5. Logistic model outputs of habitat-use and deer trail analyses. Displayed models include all the retained models with ΔAIC<6, whilst omitting models that represented more complex versions of retained nested models. Habitat use was tested against both surfaced/unsurfaced paths (PATH1) and surfaced-paths only (PATH2) in the HA. Deer trails were tested against surfaced/unsurfaced paths in the HA. Model fit was measured against null models by Wald x^2 tests, shown in grey.

Retained Models		*AICc*	*ΔAICc*	*n*	*LL*	Wald x^2 Tests		
PATH1 HA						*Wald* x^2	*d.f.*	*P*
Model 1	HAB + PD + PV + SAC	756.0	0	1157	-373.954	27.862	4	<0.001
Model 2	HAB + PD + SAC	757.6	1.62	1157	-375.779	24.21	3	<0.001
PATH2 HA								
Model 1	HAB + PD + PV + SAC	756.0	0	1157	-379.494	31.485	4	<0.001
Model 2	HAB + PD + SAC	756.6	0.61	1157	-378.784	21.416	3	<0.001
IB								
Model 1	SEASON + PV + SAC	395.5	0	310	-194.694	11.406	3	0.003
Model 2	SEASON + SAC	396.8	1.31	310	-194.18	8.059	2	0.004
DEER TRAILS								
Model 1	HAB + SLO	1007.9	0	1157	-499.908	40.737	3	<0.001
Model 2	HAB	1018.9	11.08	1157	-506.454	26.992	2	<0.001

† PD and PV represent Distance to the nearest path (m) and Visibility of the nearest path, respectively. HAB represents Habitat as a dichotomous categorical variable (grass/heather and bracken/moss/bog) in the first 4 models. For Deer Trails, HAB Habitat in 3 variables (bracken, grassland/bracken mixed and bog/moss/heather). SAP represents spatial- PATH1 represents the modelling of habitat plots against both surfaced/unsurfaced paths, and only surfaced paths are analysed in PATH2 models. Wald x^2 results were produced from comparing retained models against null models.

In the HA, habitat use was not significantly affected by the following variables: season, slope, path traffic, and distance to the nearest woodland or the type of nearest woodland. No interaction terms were retained in the analysis. There was no evidence of a non-linear effect through comparing plots within buffers against all other plots. Excluding un-surfaced paths from the analysis did not change which predictors were retained; the best models selected under both PATH1 and PATH2 analyses were consistent in terms of predictors and the associated direction of effects. Path visibility, distance to the nearest path, SAC and habitat type were retained in the best model (ΔAIC = 0); however, a simpler model that featured distance to path and habitat type was retained (PATH1: ΔAIC = 1.62; PATH2: ΔAIC = 0.61), suggesting that path visibility is a relatively unimportant predictor of habitat use (Table 4.5).

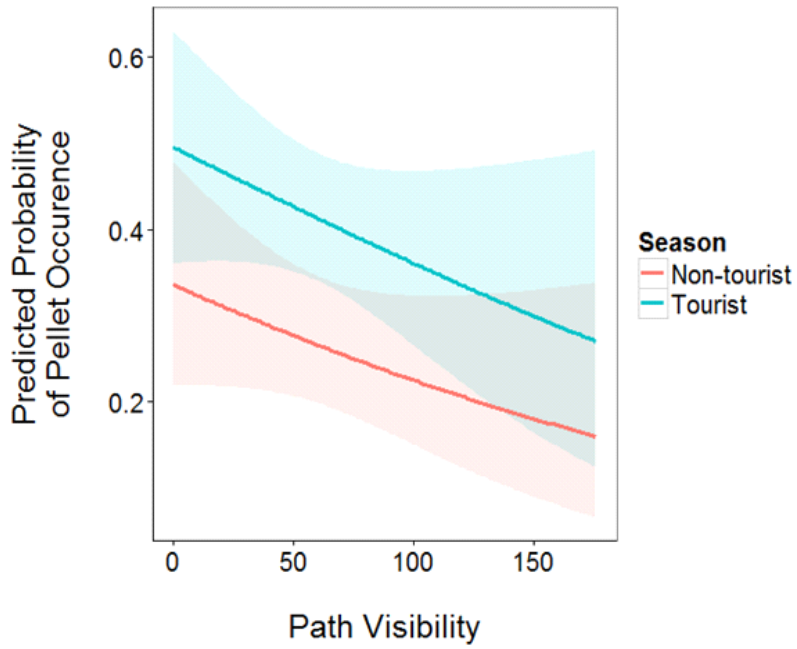


Figure 4.3. The effect of path visibility on the predicted probability of observing pellets in habitat plots in the non-tourist season (red) and tourist season (blue) in the IB. Visibility refers to the visibility of the nearest path from a given habitat plot. The interactive term of season with path visibility was not retained in any model. Shaded areas represent 95% CIs.

Of the habitat categories, pellet presence was statistically higher in G, HMG, and H habitats than in B, Br, MG, and GB habitats (Figure 4.4.). For both PATH1 and PATH2 analyses, both distance to the nearest path and path visibility (when retained) share a significantly positive relationship with habitat use (Figure 4.4; Table 4.5.). In the PATH1 analysis, assuming no change in path visibility or habitat, the log odds of recording pellet presence increase by 0.13% for every additional metre away from the nearest path. Assuming no change in distance to the nearest path or habitat type, the log odds of observing pellets increase by 0.16% for every one-unit increase in path visibility. The predicted probability of observing pellet presence is 0.52 in G/HMG/H habitats, and 0.37 in B/Br/MG/GB habitats.

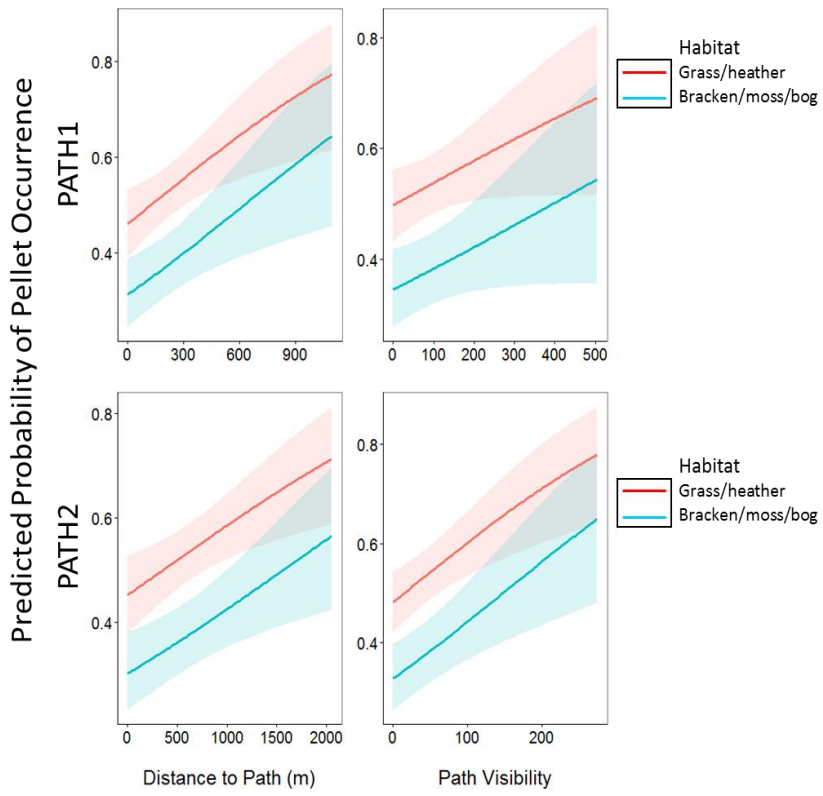


Figure 4.4. The effect of distance to path (right) and path visibility (left) on the predicted probability of observing pellets in habitat plots in grass/heather habitats (red) and bracken/moss/bog habitats (blue) in the HA. The top row shows the effects of both surfaced and non-surfaced paths, whilst the bottom row shows the effects of surfaced paths only. Interactive terms of habitat with either path metric were not retained in any model. Shaded areas represent 95% CIs.

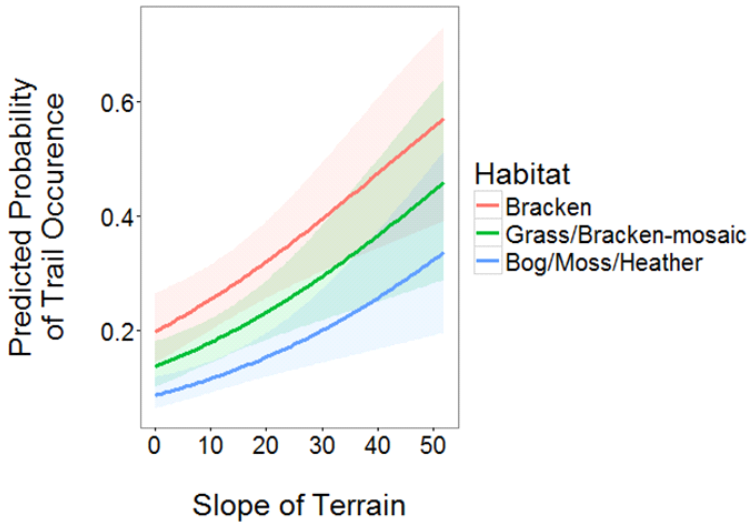


Figure 4.5. The effect of slope of terrain on the predicted probability of observing deer track presence in habitat plots in bracken (red), grass/bracken-mosaic (green) and bog/moss/heather (blue) habitats in the HA. Interactive terms of habitat with either path metric were not retained in any model. Shaded areas represent 95% CIs.

Two models were selected for predicting the presence of deer tracks. The best model for predicting deer tracks retained habitat type and slope (ΔAIC = 0), and habitat type featured as the sole predictor in the second model with a ΔAIC of 11.08 (Figure 4.5.; Table 4.5.). Of the habitat categories tested, deer trail presence was significantly influenced by the following habitats from highest to lowest influence: B habitats; G and Br habitats; and lastly GB, MG, H, and HMG (Figure 4.5.). In the best model, assuming no change in habitat type, the odds of observing a deer track in a plot increase by 3.29% for every additional degree in slope. The predicted probabilities generated from the best model of observing deer track presence are 0.26 for bracken habitats, 0.18 for grassland/bracken mixed habitats, and 0.119 for bog/moss/heather habitats.

4.3.4. TEMPORAL PATTERNS IN PATH USE

During the non-tourist season, only one incidence of deer using the path systems was found in the HA, and no incidences of deer use were photographed in the IB. As such, it was not statistically feasible to compare the path use of deer between seasons. All results reported are entirely based on data collected during the tourist season. The number of records for deer and tourists across both IB and HA sites, and within both sites in the HA are given in Table 4.5. Between sites, the IB and the HA represented the fewest and most number of records collected for tourists and red deer, respectively. Kernel density estimator Δ_4 was reported for the HA site and for the west-path site within the HA, as in both cases the smaller sample had more than 75 observations. The opposite was true of the IB and the near path site within the HA, and so Δ_1 estimates were reported.

Within the HA, the east and west site represented the fewest and most number of records collected for red deer, respectively. Tourist and deer path use peaked at similar times for both the HA and IB (Figure 4.6.). In both sites, tourist path use peaked sharply slightly after midday, and was defined by the first and last timings of the ferry crossing (HA= 77% of observations were between 09:00 and 17:00; IB = 84% of observations were between 09:00 and 17:00). A less notable peak of tourist path use occurred slightly after 18:00, which was more obvious in the HA than the IB (HA= 12% of observations between 17:00 and 19:00; IB = 9% of observations between 17:00 and 19:00). In both sites, deer exhibited a bimodal pattern of path use, being photographed mostly at night/dawn, and again to a lesser extent at dusk (HA: 53% of observations between 01:00 and 07:00, and 36% of observation between 18:00 and 00:00;

IB: 63% of observations between 01:00 and 07:00, and 39% of observation between 18:00 and 00:00). Estimated overlap coefficients indicate that tourists had a higher degree of overlap with deer in the HA site (($\Delta_4$0.18) than the IB site ($\Delta_1$0.07; Figure 4.6.).

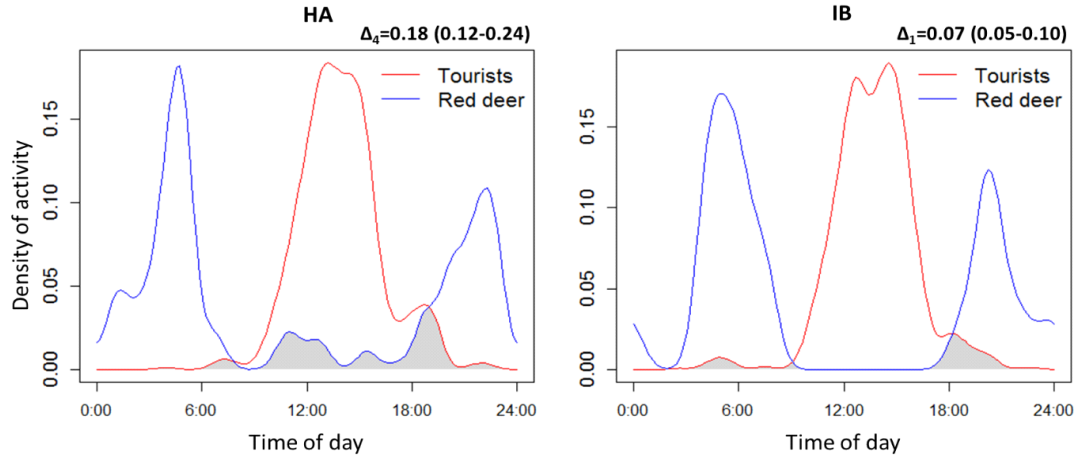


Figure 4.6. Estimates of the daily patterns of tourist and red deer path use in the HA (right) and the IB (left). Lines in red are the kernel-density estimates for tourists, and lines in blue are the kernel estimates for red deer, derived from photograph times. The overlap coefficient between the two kernel-density estimates is represented by the grey area in each plot. Figures in top-right of each plot indicate the overlap coefficient, with 95% CIs derived from 10000 bootstraps in parentheses. Average time of sunset was 0410 hours, and average time of sunset was 2120 hours during the study.

Within the HA site, observations of both tourists and deer recorded at the west site mimic the patterns of path use exhibited by the HA site in totality, and the east site also exhibited a similar temporal pattern of tourist path use, but patterns of deer path use differ (Figures 4.6. and 4.7.). At the east site, deer were observed on the path systems during dawn (74% of observations between 01:00 and 07:00), but the second bout of path use found in other locations was markedly reduced (12% of observations between 18:00 and 00:00). Estimated overlap coefficients indicate that tourists had a higher degree of overlap with deer in the end site ($\Delta_4$0.20) than the start site ($\Delta_1$0.14; Figure 4.7).

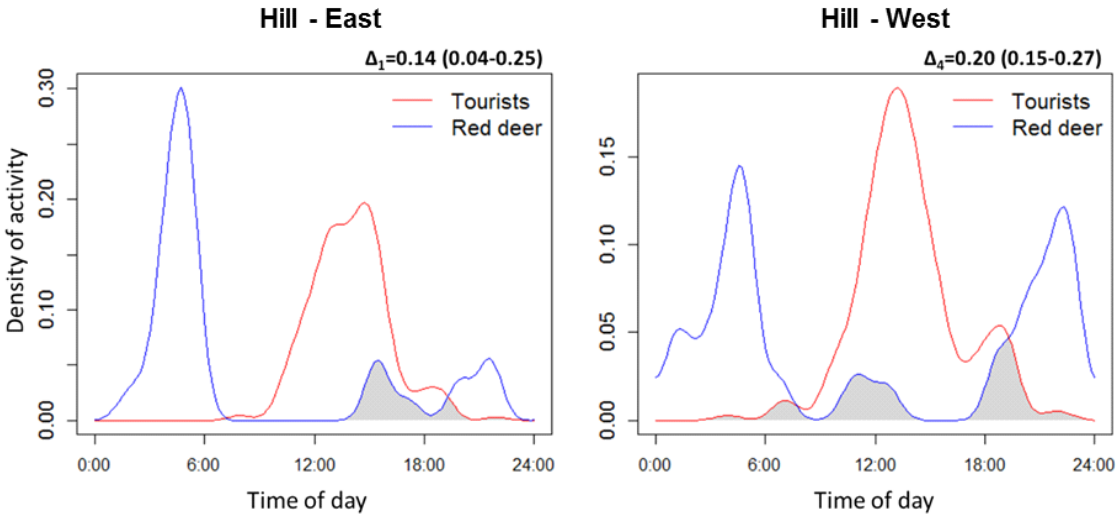


Figure 4.7. Estimates of the daily patterns of tourist and red deer path use at paths close to the HA entrance (right) and far from the HA entrance (left). Lines in red are the kernel-density estimates for tourists, and lines in blue are the kernel estimates for red deer, derived from photograph times. The overlap coefficient between the two kernel-density estimates is represented by the grey area in each plot. Figures in top-right of each plot indicate the overlap coefficient, with 95% CIs derived from 10000 bootstraps in parentheses. Average time of sunset was 0410 hours, and average time of sunset was 2120 hours during the study.

Table 4.6. Total numbers of camera trap records of tourists and red deer between sites, and within the HA site (near and far), alongside estimates of path-use pattern overlap between tourists and red deer in both the HA and the IB, with approximate 95% bootstrap confidence intervals given in parentheses.

	STUDY AREA			
	IB	**HA[a]**	**HA- START**	**HA - END**
Tourists	915	591	402	189
Red deer	49	185	34	151
Overlap of activity patterns	Δ_1=0.07 (0.05-0.10)	Δ_4=0.18 (0.12-0.24)	Δ_1=0.14 (0.04-0.25)	Δ_4=0.20 (0.15-0.27)

HA[a] represents the HA site in its entirety (HA-START & HA-END).
The estimator of overlap of path use between tourists and red deer was Δ_1 if the sample size of at least one of the densities measured was lower than 75, and Δ_4 was used if the sample sizes of both densities exceeded 75.

4.4. DISCUSSION

4.4.1. INFLUENCE OF PATH SYSTEMS ON HABITAT USE

Paths can fragment the landscape and induce avoidance behaviour, resulting in habitat loss and consequent reductions in carrying capacity (Nellemann *et al.*, 2001). The current study indicates that, regardless of path traffic, red deer exhibited strong avoidance behaviour towards both way-marked trails and surfaced paths in the HA, whilst path proximity did not affect habitat use in the IB. Furthermore,

whilst path visibility influenced habitat use in both sites, the direction of the effect was not consistent; habitat use was positively influenced by path visibility in the HA, and a negative relationship was revealed in the IB. Ungulate responses to path/road proximity differ between studies and species (Laurian *et al*., 2008, Rowland *et al*., 2000). Rost and Bailey (1979) compared the distribution of red deer and mule deer (*Odocoileus hemionus*) in relation to roads between two sites, and found mule deer to avoid roads consistently whereas red deer avoided the roads in only one site. Paths may be avoided for multiple reasons, including the unnatural surface of the path, the openness created by the clearing of vegetation, and an association with human activity (Meisingset *et al*., 2013). Deer experience higher levels of human activity in the IB than in the HA, and the contrasting effects of path visibility and distance on habitat use between the sites may point to a difference in habituation to human activity, as discussed in **Chapter 3**. Ungulates are known to favour areas that offer suitable vantage for detecting potential predation (Hochman and Kotler, 2007), and this might explain habitat selection in the HA. In associating paths with human presence, deer occupy habitats that provide a line of sight to a source of known disturbance, but are far placed from the source of disturbance.

In the IB, the lack of a proximity effect on habitat use could be explained in part by the abundance of accessible refugia in the form of woodland in this area. Open land/forest edge has the benefit of exposing potential predation in the open land to ungulates, and the woodland provides an escape route if necessary (Geist, 1998). Although not quantified, deer in the IB were observed to flee routinely into the woodland when encountered by researchers. In the IB, the maximum distance of a habitat plot from the nearest woodland was 180m. Red deer may perceive that this is within the threshold of safe distance from refugia, and consequently all areas studied receive similar levels of habitat use. This also would explain why distance to woodland did not affect IB habitat use. It is unclear why deer favoured areas with low path visibility in the IB. It was expected that habituation to the high level of human activity would manifest by path visibility having no influence upon habitat use. Pelletier (2014) examined how trail-users in an ecotourism setting affect the habitat-use patterns of bighorn sheep (*Ovis canadensis*) and three cervid species: moose (*A. alces*), white-tailed deer (*O. virgianus*) and elk (*C. elaphus canadensis*). For all species, high traffic reduced the use of areas that were visible from the paths, and furthermore, were more likely to occupy terrain that facilitated escape. Erroneous results may have arisen from overly simplistic spatial analyses. When calculating path visibility, woodland was incorporated into the analysis as an

opaque feature, i.e. completely blocking the line-of-sight from a given habitat plot to the nearest path. In reality, deer may be able to visualise a path positioned behind woodland, depending on the density of trees and the distances involved. Moreover, audio and olfactory signals will be sensed by deer, which may contribute to patterns of habitat use. These factors could be implemented into creating a path visibility metric in a more complex and realistic analysis. Alternatively, whilst the FAR analysis proved that recorded pellet counts represented the habitat use of the period that data collection took place, it was impossible to detect the presence of finer temporal patterns in habitat use. Habitat selection in red deer varies throughout the nychthemeron, and deer have been shown to exploit exposed habitats during the night, since cover is provided by a lack of light (Godvik *et al*., 2009). A similar process may occur in the IB, whereby deer forage with close proximity to the woodland during the day, and exploit all areas of the pastures later when tourists have left the island. This could result in a spread of pellets throughout the pasture and the effects of path proximity would not be apparent.

4.4.2. INFLUENCE OF HABITAT CONDITIONS ON HABITAT USE

Habitat use was higher in forage-rich heathlands and grasslands than in the resource-poor bracken, moss and bog habitats (Clutton-Brock *et al*., 1982). The grassland habitats in this study feature *Agrostis* and *Festuca*, which are known to act as an important source of protein-rich forage for red deer (Osborne, 1984). Bog habitats, of which *Juncus* rushes are predominant contribute little to the diet of red deer, explaining the relative lack of use of these habitats (Clarke et al., 1995a). The heathland category was formed from combining heather and heather-moss-grass mosaic habitat types. In conjunction, these habitats represent large areas of heather interspersed with patches of *Molinia* grassland. Whilst *Molinia* is generally not grazed by deer, these habitats are visited often as deer search between the *Molinia* tussocks for the broad-leaved grasses found in this vegetation community (Osborne, 1984). Furthermore, heather itself is an important item in the diet of red deer (Clarke et al., 1995a). It is likely that habitat use was lower in bracken habitats as bracken offers poor-quality forage (Grant *et al*., 1981), and presents physical resistance to locomotion.

There was no evidence that the path proximity effect differed with habitat type in the HA. Previous studies have shown that habitats that provide cover and/or high forage-availability influence avoidance behaviour towards road systems (Jayakody *et al*., 2008, Meisingset *et al*., 2013). Gagnon *et al.*

(2007) found that red deer were more likely to tolerate roads when high-quality foraging areas were nearby. Whilst the height profiles of the different habitats studied were not quantified, the absence of an interactive effect between path proximity and habitat may be due to a lack of structural differences between habitat types. In comparison to Jayakody *et al*. (2008) and Godvik *et al*. (2009), no habitat type would have provided ample cover from the path systems.

4.4.3. INFLUENCE OF SEASONALITY ON HABITAT USE

In the HA, habitat selection was not influenced by seasonality. Previous studies have shown that red deer shift habitat selection with respect to seasonal variation in forage quality and abundance (Clutton-Brock *et al*., 1982). At northern latitudes, forage availability and quality varies seasonally (Albon and Langvatn, 1992). Generally, grasslands are favoured during the warmer months due to the high forage quality of these habitats, whilst forest habitats are selected in the winter months (Godvik *et al*., 2009) as these provide refuge from adverse weather, especially snow cover, and the associated energetic demands for locomotion (Parker *et al*., 1984). On Ulva, there was no snow cover present during data collection, and the island seldom experiences persisting snow cover (J. Howard. per. comms.). Furthermore, there is little woodland in the area studied to accommodate a notable shift in red deer habitat preference. Perhaps the lack of woodland explains the absence of seasonal shifts in habitat selection.

Surprisingly, habitat use was higher at study sites during the tourist season in the IB. Given that the tourist season features an increase in human activities, it was expected that habitat use would be lower during this period. However, rather than human activity explaining this seasonal effect; the same rationale used to explain the absence of seasonal influence in the HA can be applied to account for the seasonal shift found in the IB. Whilst there was no woodland in the HA for red deer to utilize during the winter months, there is an abundance of woodland in the IB, and a decrease in habitat use during the IB reflects a switch in preference from pastures in the summer towards woodlands in the winter. Whilst this seasonal shift in habitat selection is documented in the literature (Clutton-Brock *et al*., 1982, Godvik *et al*., 2009, Jayakody *et al*., 2008), it should be noted that habitat use in woodlands was not quantified. However, as woodland represents the majority of non-pasture habitat in the IB, a decrease in pasture use should correlate with an increase in woodland use.

4.4.4. INFLUENCE OF HABITAT TYPE AND SLOPE ON THE FORMATION OF DEER TRAILS

Deer trail presence was positively related to sloping terrain, and three habitat groups were found to influence trail presence, listed in order from least to most influential: bog/moss/heathlands, grass/grass-bracken mosaic, and bracken habitats. Deer trails have been used to index habitat use (McCaffery, 1976) and population density (Mech *et al*., 1980). Here, deer trail and pellet presence was subject to the same statistical model, yet different processes were found to explain the occurrence of each. Therefore, using trails and pellets as proxies of habitat use yields contrasting results. For example, trail data suggests that deer strongly select bracken habitats, whilst pellet data shows the very opposite to be true. In this study, deer trails are rejected as indices of habitat use for several reasons. First, deer deposit pellets regardless of behaviour (albeit at different rates depending on the behaviour), but trails specifically denote locomotion behaviours. Second, the differences in trail presence found between habitat types likely reflect differences in the susceptibility of the ground flora to trampling damage, rather than habitat preference. Therefore, trails are likely to produce misleading results in indexing habitat use.

It is not surprising that steep terrain positively influences deer trail occurrence. Red deer engage in daily altitudinal shifts in a crepuscular rhythm, descending to lower ground at dusk and retreating to higher altitudes after dawn (Clutton-Brock *et al*., 1982). Herds negotiate through adverse terrain by choosing the most accessible route in single file formation. Over time, repeated trampling compresses the vegetation, furthering the accessibility and preference of the route for deer. This process eventually leads to the complete removal of vegetation and the formation of a trail. This could also explain the significant occurrence of deer trails in bracken habitats, as deer may be limited by their movements through the obstructive vegetation. On more even ground, there is less need for deer to navigate through the terrain via the most energetically cost-effective pathway, and trampling is not constrained to a specific area as deer do not traverse over the same route each time.

4.4.5. TEMPORAL OVERLAP OF RED DEER AND TOURIST PATH-USE

The temporal overlap of human activity with that of wildlife has been previously investigated in Carter *et al*. (2012), whereby similar methods were employed to show that peaks of human activity in a national park caused a shift in the temporal patterns of activity in resident tigers (*Panthera tigris*).

However, the current study assessed explicit path-use behaviour as opposed to overall activity, and in doing so this chapter presents the first study to quantify the temporal patterns of path-use in red deer, and furthermore, to assess the degree of overlap in these patterns with that of human path-use. These results provide a temporal perspective on the use of path systems by wildlife and tourists, which supplements previous research on the relationship of path systems and associated tourist activity with red deer behaviour (Jayakody et al., 2008, Sibbald et al., 2011b).

It is surprising that only one instance of deer path-use was recorded during the non-tourist season, since tourist-use of the path is largely reduced at this time of year. Furthermore, the results from the inter-site study in the HA suggest that deer respond to less tourist traffic by increasing path use. Winter path use was investigated in early December, which roughly coincides with the end of the rutting period (Clutton-Brock *et al*., 1982). Stags cease to feed during the rut, causing a severe drop in body weight (Mitchell *et al*., 1976). Furthermore, seasonality has significant implications on hinds and calves, by which energy-saving strategies are adopted in response to inclement weather and comparatively low availability of quality forage during the winter (Loison and Langvatn, 1998, Schmidt, 1993). It may be because during the winter season the height of obstructive vegetation such as bracken is relatively reduced in comparison to the summer season. In which case, the paths are less of an attractant as the whole landscape is now easier to traverse at this time of year.

The results here showed a clear contrast between deer use and human use of the path at all sites. Unsurprisingly, the majority of human path-use in all sites was between 0900hrs and 1700hrs, given that those times represent the first and last ferry crossing, respectively. All sites feature a secondary peak of human path-use, which occurred slightly after 1800hrs. This was almost entirely comprised of routine activities carried out by the local residents of Ulva, such as dog-walking and farming necessities. Deer were observed to use the path with mutual exclusivity to the temporal pattern of human path-use in both the HA and the IB, but a stronger degree of overlap in path-use was found in the HA than the IB. This is a small difference, and is potentially a product of the IB being a much smaller site and closer to the ferry access point, allowing deer to more accurately predict when tourist activity ceases for the day. This argument is further supported by the larger overlap found at the end HA site than at the start. This is the furthest point from the ferry access studied, and receives fewer tourists, so it would be harder for deer to predict the cessation of tourist activity.

For all sites, deer presence peaked at approximately 0500hrs and again at 2100hrs. These timings correlate with the crepuscular nature of deer activity (Clutton-Brock *et al*., 1982). Path-use may facilitate the daily altitudinal shifts in habitat use characteristic to the species i.e. descending from high altitudes in the evening, and returning to higher ground the following morning. The same patterns of path use were found for the IB, but since this site features little altitudinal variation, it is likely the paths are used as travel corridors through otherwise relatively harsh woodland.

4.4.6. CONCLUDING REMARKS

Responses to the path systems show clear differences depending on the sites studied. In the HA, deer spent more time in grasslands and heathlands that are far from the path and provide clear vantage of the path systems. This indicates that deer in the HA are not habituated to tourist activity, and select areas in favour of detecting human presence from a perceived safe distance. This displacement has a lag effect, persisting through the winter period when tourist activity is at a minimum. In the IB however, deer did not exhibit any preference for habitats further away from the path systems. This could be due to habituation to human activity in the IB by greater human activity, or that the disturbance impact of tourists is reduced by the constant proximity to refugia in the form of woodland.

Both populations utilized the path systems during low periods of human activity. These path-use results show that path avoidance in the HA must be temporal, as paths were used both in the morning and in the evening. As such, habitat use changes throughout the 24-hour cycle, as deer must reduce path avoidance as they approach the path systems during these times. Therefore, regardless of whether or not deer are habituated to human activity, deer can adapt to the conditions of the disturbance. In this case, deer adapt to the timing of tourist activity, and benefit from the source of the disturbance by using the path to reduce energy expenditure in traversing the landscape.

CHAPTER 5

MULTISCALAR ANALYSIS OF HABITAT CONDITIONS AND DEER ACTIVITY IN DETERMINING THE PRESENCE OF A RARE DAY-FLYING MOTH

'Like splendour-winged moths about,

a tapor.'

- P.B. Shelley

5.1. INTRODUCTION

Burnets (*Zygaena* Fabricius 1775) form a genus of day-flying, aposematic moths with a Palaearctic distribution, and are notably similar in biology to many butterfly species (Niehuis *et al*., 2007, Tremewan, 1985). Burnet species typically display limited mobility, and seemingly occupy small areas (Tremewan, 1985). When suitable habitat is present, species can occur abundantly and can be observed feeding on flowers frequently, and often tend to be the dominant pollinators (Franzén and Ranius, 2004). The population structure of burnets is similar to the metapopulations formed by many butterfly species (Bourn, 1995, Franzén and Ranius, 2004).

Many British macro-moth species are experiencing severe long-term population declines, implicating a nation-wide deterioration of suitable habitats as the main driver (Conrad *et al*., 2006). Burnet moths are not exempt from reductions in the availability of suitable habitat, and have thus experienced population declines throughout Europe (Sarin and Bergman, 2010). Whilst studies on the taxonomy and systematics of *Zygaena* are extensive (Hofmann and Tremewan, 2010), the ecology and behaviour of burnets is poorly understood in comparison to butterflies, and this is evident in the current lack of knowledge of the distribution of many European species (Bourn, 1995). Despite European population declines, the family are yet to feature on international red lists (Franzén and Ranius, 2004). Generally, zygaenids inhabit dry grasslands, and semi-natural pastures are an important habitat in particular (Franzén and Ranius, 2004). Throughout Europe, these semi-natural grassland habitats have been in severe decline since the early 20th century (Sarin and Bergman, 2010).

There are 97 species in the *Zygaena* genus, of which 7 species are represented in Britain. The slender scotch burnet (*Z. loti*), new forest burnet (*Z. viciae*), and the narrow-bordered five-spot burnet (*Z. lonicerae*) are currently restricted to the west coast of Scotland (Hofmann and Tremewan, 2010). Many British insects exhibit extremely restricted distributions (Ravenscroft and Young, 1996b), and in the case of burnets, isolated populations persist in north-west Scotland, far removed from their main ranges occurring in southern England or on the European continent (Thomas, 1995), and it is remarkable that these populations persisted in such restricted areas (Ravenscroft and Young, 1996b). It is presumed that species exhibiting these curious distribution patterns colonized Britain following the retreat of the last ice sheet in 12000 BC (Dennis, 1977). A period of relative warmth occurred around 4-5000BC, and this process relaxed ecological constraints, allowing for the colonization of north England and Scotland

(Ravenscroft and Young, 1996b). As the climate cooled again, populations were restricted to relatively warm refugia. For burnets, exceptionally favourable habitat conditions exist in western Scotland, and the richness of *Zygaena* in this region is attributed to both the climatic variation within and between the Hebridrean Islands (Bourn, 1995). First, certain rare burnet moth species depend upon basalt outcrops, and these occur extensively on the Isle of Ulva, Mull, smaller islands nearby and the Ardnamurchan peninsula on the mainland (Drury, 1973). These basalt coastal cliffs influence the growth of herb-rich vegetation communities that support various burnet foodplants, e.g. bird's foot-trefoil (*Lotus corniculatus*) for slender burnets (*Z. loti*), and wild thyme (*Thymus serpyllum*) for transparent burnets (*Z. purpuralis*) (Ravenscroft and Young, 1996b). Second, south-facing slopes benefit from prolonged sun exposure, and this heat is retained by short-sward grassland, low-lying forbs and bare soil, and sheltered from wind by the basalt cliffs. In addition to these species-specific conditions, the Inner Hebrides experiences a particularly mild and constant oceanic climate, and the area acts as a stronghold for other British Lepidoptera in decline (Warren, 1994), such as the marsh fritillary (*Eurodryas aurinia*) and the arctic skipper (*Carterocephalus palaemon*). Furthermore, the persistence of these isolated populations can be attributed to the absence of historical land management practices that led to the extirpation of populations elsewhere (Ravenscroft and Young, 1996b). Intensive agriculture was not viable in the region, and this allowed for the existence of a diversity of habitats (Wormell, 1983).

5.1.1. RESEARCH AIMS AND OBJECTIVES

On Ulva, the south/south-east facing slopes of the HA coastline are inhabited by Z. *filipendulae*, *Z. loti* and *Z. purpuralis.* The short-sward grasslands found on these slopes are biodiverse, supporting an array of herb-rich microhabitats, and are therefore of conservation interest. Conservation management schemes of grasslands typically focus on promoting the grazing-dependant flora of these habitats. However, this management approach typically uses grazing regimes that are too intense and do not benefit the persistence of other taxa that inhabit semi-natural pastures (Franzén and Ranius, 2004), and conservation management should, instead, adopt more holistic measures with respect to insects. However, in being the most species-rich taxon, the requisites of compiling an inventory of insect diversity and associated habitat requirements are often too costly and time-consuming for management budgets. Herein lies the utility of bioindicators: easily-recognisable species that by correlating with a total high biodiversity

can be used to predict species richness. Burnet moths are proven to be apposite bio-indicators of herb-rich, biodiverse grasslands and are assoicated with overall insect species richness (McGeoch, 1998). For example, Franzén and Ranius (2004) verified the potential of burnet moths as bioindicators, finding that the total number of burnets present in an area was positively correlated with butterfly richness, and to a lesser extent, vegetation richness. However, the authors state that the use of burnets as bioindicators is confounded by a lack of knowledge on burnet ecology, specifically on the spatial and temporal scales at which habitat selection operates.

Regarding the biodiverse grassland slopes of Ulva, there are several factors that make *Z. purpuralis* an appropriate bioindicator. *Z. purpuralis* is more readily found than the rare and declining *Z. loti*, but shares similar microhabitats: early-successional short-sward, herb-rich grasslands (Burman et al., 2014, Clausen et al., 2001, Franzén and Ranius, 2004, Ravenscroft and Young, 1996b, Sarin and Bergman, 2010). Additionally, burnet moths are an easy family to study in general due to ease of recognition in the field, in possessing relatively sedentary habits, weak-flying abilities and exhibit fearlessness when approached (Franzén and Ranius, 2004). In using *Z. purpuralis* as a bioindicator, the aims of this chapter are twofold. First, to ascertain the importance of specific habitat characteristics such as plant composition, diversity and structure in determining *Z. purpuralis* densities, and to consider the importance of scale in determining habitat selection Second, this study aims to investigate the relationship of deer behaviour and habitat use with overall diversity. A novel technique of pheromone-baited funnel traps will be employed to address these aims. The application of pheromone-baited traps as an ecological monitoring tool has generally been limited to quantifying the presence of pest populations. Extending the utility of pheromone-baited traps to monitor rare and declining *Zygaena* populations, in addition to determining suitable habitat locations and habitat continuity has been proposed (Burman *et al*., 2014), but there are no respective studies published to date. Priesner *et al*. (1984) reported the use of species-specific pheromones for several *Zygaena* moths, including *Z. purpuralis*, the female pheromones of which were hitherto unknown. Several isolated populations were tested, and the attractants proved to elicit behavioural responses in male moths identical to those typically observed in response to conspecific females. Furthermore, the number of male moths attracted to a given lure was correlated with the total number of moths of the population tested. As such, sampling a species in this manner could provide a viable estimate

of the local abundance or density. In this study, pheromone traps are used in conjunction with traditional ecological fieldwork methods to make such inferences about species ecology.

Objective 1: Traditionally, research on Lepidopteron metapopulations has focused on the size, abundance and relative isolation of suitable habitat patches, whilst studies carried out on a smaller scale have focused on the quality of those habitat patches on an individual basis (Sarin and Bergman, 2010). The relative importance of habitat quality, size and isolation is a contentious issue, and recent studies encourage the consideration of all factors in conservation management (Dennis *et al*., 2003, Sarin and Bergman, 2010). For weak dispersers such as burnets, suitable habitat typically includes resources that can support each life stage (Anthes *et al*., 2003). Whilst imago foodplant abundance is critical in ensuring population persistence, imago distribution and abundance is typically dependent on the presence of the highly specialised habitat conditions required by eggs, larvae and chrysalises (Thomas, 1984). In the case of *Z. purpuralis*, egg batches are laid on *Thyme* or other low-lying forbs found in sheltered hollows on the ground, or in close proximity to bare soil (Bourn, 1995). From this, it was expected that *Z. purpuralis* abundances would be higher in areas with bare soil and high cover of *Thyme*. To test this, pheromone baited funnel traps were placed throughout the short-sward grasslands, and catch rates were related to a series of vegetation metrics collected at different scales.

Objective 2: The conservation of these grasslands is largely dependent on grazing pressures maintaining an early successional stage. Due to the remote location of these habitats on the island, they were seldom grazed by livestock. Regardless, it was likely that these habitats experienced grazing from free-ranging red deer. However, the relationship that deer may have had with these habitats was unknown. Therefore, in using pellet counts as an index for habitat use, the number of deer pellet groupings surrounding trap sites were related to *Z. purpuralis* catch rates. Additionally, the presence of deer trails at trap sites were related to catch rates, as these habitat features may have provided a significant source of bare soil, an important condition for favorable egg-laying sites.

5.2. METHODS

5.2.1. SPECIES BIOLOGY

Z. purpuralis have an univoltine imago form, occuring from early June to July, and it inhabits steep, south-facing grassy slopes on coastal cliffs or inland limestone areas (Tremewan, 1985) that feature

Thyme, the larval hostplant and favoured adult foodplant (Bourn, 1995, Wormell, 1983). The west-coast of Scotland features the largest population of *Z. purpuralis* (Tremewan, 1985). Two subspecies of *Z. purpuralis* occur throughout the British Isles: subsp. *sabulosa* is distributed throughout the Burren district of County Clare and County Galway, its range extending westwards onto the Aran Islands; and subsp. *caledonsis*, the more common of the two subspecies, is distributed throughout the Inner Hebrides, often locally abundant on Skye, Rhum, Canna, Muck, Eigg and Mull, in addition to coastal areas on Argyll, extending northwards from Ardnamurchan from its most southerly location, the Mull of Kintyre (Tremewan, 1985, Wormell, 1983). Historically, subsp. *segontii* existed in small colonies on cliffs along the coastline of Caernarvonshire in Wales, but there have been no recorded sightings since 1961 and is now likely to be extinct (Hambler and Speight, 1996). On Ulva, the species is limited to sloping grasslands located on a small portion of coastline in the HA, shared by *Z. loti* and *Z. filependulae* (J. Howard pers. comms.).

5.2.2. FIELDWORK AND GIS PROTOCOL

Locations for placing funnel traps were derived from surveys and from anecdotal information (pers. comms. J. Howard). A 1.5km stretch of coastline in the HA with sloping grasslands was chosen as the study area. 22 funnel traps baited with female *Z. purpuralis* pheromone were placed randomly along the coast at approximately 80mamsl (Figure 5.1). Traps were placed at least 50m apart to ensure that trap catchments were independent. Traps were baited on alternate days. On trapping days, traps were baited with the pheromone lure at 1800hrs, when most insect activity had ceased for the day. After 24 hours, moths inside the trap and within a 5-m radius of the trap were counted and the captive specimens were released. Wind speed was recorded by a Kestrel 1000 at a 0.4m/s resolution held at trap height, and these values were averaged to create mean wind speed for each trap location. The pheromone lures were then removed from the traps until the following day to prevent excessive disruption to the breeding season.

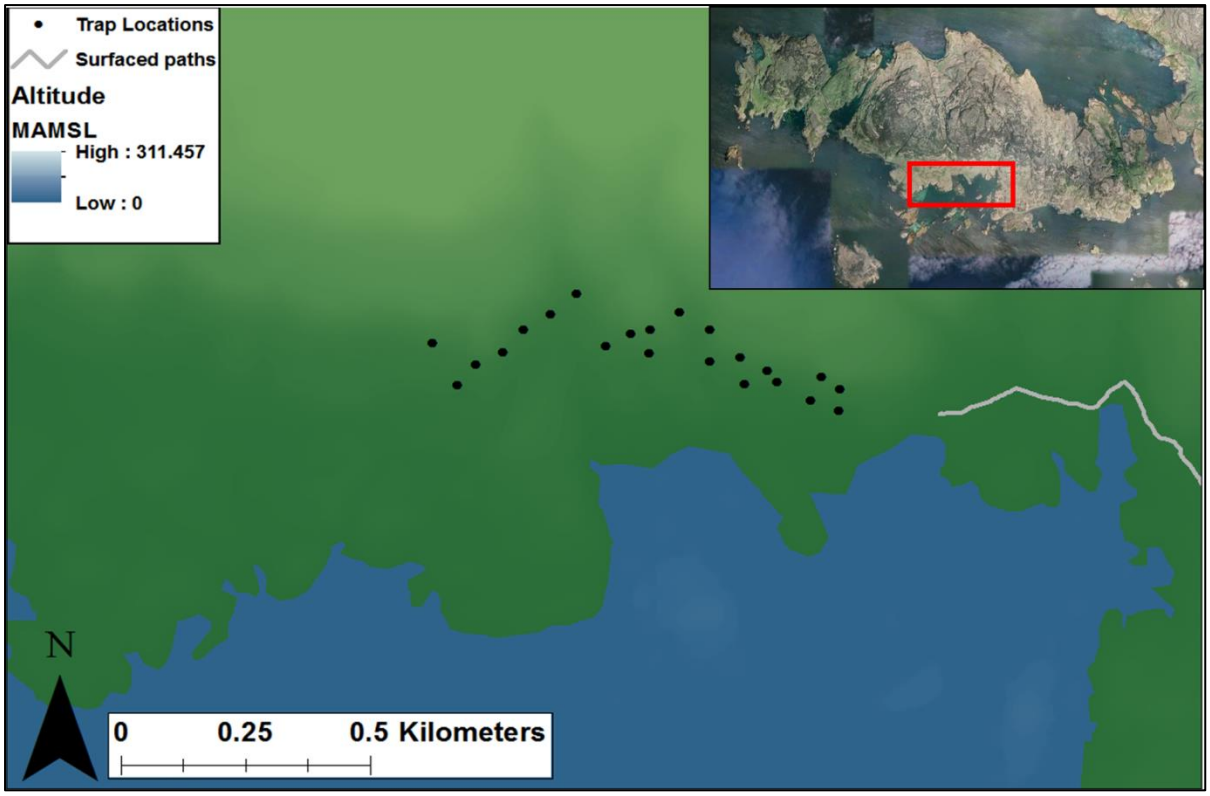


Figure 5.1. Locations for each of the 22 pheromone-baited funnel traps within the HA relative to the Isle of Ulva. Traps were placed from east to west loosely along a transect that alternates between a low slope site and a high slope site, however final locations were limited by the extent of grassland habitat.

As moths are relatively mobile insects, pheromone lures could potentially attract individuals from a range of distances. Therefore, catch-rates represent the quality of local habitat in addition to the abundance and/or quality of habitat patches further afield. To account for this, variables were recorded at four different scales: $2m^2$, $5m^2$, $10m^2$, and $50m^2$ radius. The dimensions of the $2m^2$ plot were delineated by the same method used for habitat plots in **Chapter 4**. The following variables were recorded within the 2m radius: the occurrence of all plant species, and of exposed soil and rock, was recorded within a $2m^2$ quadrat and represented as percentage cover. 21 species/cover types (including bare soil and rock) were recorded, of which 11 were found at statistically analysable frequencies and were used in analysis: velvet grass (*Holcus mollis*); tormentil (*Potentilla erecta*); bird's foot trefoil (*Lotus corniculatus*); wild thyme (*T. serpyllum*); white clover (*Trifolium repens*); common heather (*Calluna vulgaris*); lady's bedstraw (*Galium verum*); bell heather (*Erica cinerea*); fairy flax (*Linum catharticumI*); *Fescue* spp. and *Agrostis* spp. Percentages for *Fescue* spp. and *Agrostis* spp. were pooled together to form 'short-sward' grass cover, and

C. vulgaris and *E. cinerea* were pooled into a 'heath' category. Plant diversity for sites were measured as a Shannon-Wiener Index.

At the $5m^2$ scale, the following variables were recorded: the number of blooming *Thyme* forbs, the percentage of *Pteridium aquilinum* cover, and mean vegetation height. Vegetation height was calculated by averaging 5 randomly placed drop-disc measurements within the $5m^2$ plot, whereby a 30-cm radius cardboard disc, running free on measuring tape, was dropped vertically onto the vegetation (Ravenscroft and Young, 1996b). Percentages of *P. aquilinum* were calculated by summing the cover in each constituent square metre, which were assessed with a $1m^2$ quadrat. The $10m^2$ scale was delineated by measuring tape, wherein the following variables were recorded: deer pellet presence; deer trail presence; and the percentages of *P. aquilinum*, heathland (comprised of habitat categories HMG + H, see **Chapter 2**) and short-sward *Festuca-Agrostis* grassland (habitat category G). As all plots were placed on sloping terrain, suitable vantage of the extent of the $10m^2$ scale was achieved by standing downhill of the plot. Estimates of percentage cover at the $10m^2$ scale were standardised by dividing the area into four $5m^2$ quadrants. Visual estimates of cover were made for each quadrant, and pooled together to retrieve percentage cover at the entire $10m^2$ scale. Furthermore, observer consistency was maintained for all plots. Data collection at the 50m scale was performed remotely via post-fieldwork GIS analysis; the amount of short-sward *Festuca-Agrostis* grassland within a 50m radius of each trap was calculated in two steps. Firstly, the 'Buffer' tool was used to create buffer polygons around each trap, specified in extent to 50-m. Secondly, the 'Spatial statistics' tool was used to calculate the number of short-sward grassland $5m^2$ cells pertaining to the habitat classification raster (see **Chapter 2**) that overlapped with each 50m buffer polygon. These values were then attributed to each respective trap. The aspect, slope and altitude of the terrain at each trap location was retrieved using the 'Extract to Point' tool. All GIS analysis was performed in ArcGIS 10.1.

5.2.3. STATISTICAL ANALYSES

The number of moths caught in the traps was strongly collinear with the number of moths observed outside the traps but within the $5m^2$ scale. Day-flying moths become inactive during twilight and night periods (Wipking and Mengelkoch, 1994), and as such it was probable that moths found within $5m^2$ radius of the traps were initially attracted to the pheromone, but failed to reach the trap before the late

afternoon. Under this rationale, moths found within $5m^2$ were assumed to represent the same catchment area as moths within the funnel trap. Therefore, the total number of moths within the trap and within $5m^2$ was used as the dependent variable, and tested against the aforementioned vegetative and topographic variables. At the $5m^2$ scale, vegetation height and percentage of bracken were found to be co-linear, and thus only bracken percentage was used for analyses.

From collecting daily counts of imagos, the emergence time structure can be predicted. A model was used to predict both the position of the peak emergence date but reveals the structure of the male emergence curve throughout the imago life stage. Trap counts were used to calculate the expected daily *Z. purpuralis* imago emergence counts (λ) using the following equation:

$$\lambda = \alpha \exp\left(-\frac{(d-d^*)^2}{2\sigma^2}\right)\exp\left(\beta(x-\bar{x})\right) \quad (1)$$

where d^* denotes the date when trap counts peak. The standard deviation of emergence duration is represented by σ. The average abundance of imagos is given by α, and d represents the recording day expressed as a Julian date. Generalized linear mixed-effect models (GLMMs) were used to test the topographic, vegetative and deer-related effects on *Z. purpuralis* counts. To account for the site structure of the data and account for changes in emergence patterns over the course of the imago life stage, site and recording day were included in the model as random effects. Pellet groupings were analysed as count data, as opposed to pellet presence/absence. Variables recorded at each scale were analysed against total imago abundance separately, avoiding collinearity between similar variables at varying scales, with the exception of altitude, aspect and slope, which were included at every scale to account for topographic structure in the data. Logarithmic transformations of the Shannon Weiner diversity index and $10m^2$ variables were required to meet model assumptions. Additionally, deer habitat use was related to local plant diversity by testing the effect of Shannon-Weiner index against pellet counts via an analysis of variance (ANOVA). Model selection followed the Akaike's information criterion (AIC) approach to model minimization (Richards, 2008). All models $\leq\Delta 6$ AIC are considered, whereby the most parsimonious models with the lowest ΔAIC values are retained. Additionally, models that did not represent more complex versions of simpler nested counterpart models were selected. The similarity of species composition between sites with Jaccard similarity coefficients was measured using the 'vegan' package (Oksanen *et al.*, 2007) and GLMMs were modelled with the 'glmmADMB' package (Bolker *et al.*, 2012) in R 2.15.3.

5.3. RESULTS

5.3.1. DESCRIPTIVE RESULTS AND EMERGENCE TIMES

Traps were recorded over a period of 15 days. Recording started at peak emergence of adult males (Figure 5.2). Throughout the entire field season, the south-facing slopes in the HA were investigated every 3-4 days for the first *Z. purpuralis* emergers, and recording was initiated the day after initial observations of imago activity (28/06/2015). Data collection continued until 16/07/2015, at which point moths were neither observed in the field nor caught in the traps. Nine recording days were conducted in this timeframe, but the last two days were omitted from analysis due to low moth numbers (2 and 1 moths were caught, respectively).

Predicted imago emergence timing shows that the start of the recording period coincided with peak emergence time, and the progressive decline of emergers was recorded throughout the entirety of the trapping regime (Figure 5.2). The highest number of caught males was 41 (Trap 4; Day 2). The highest total number of moths caught in one day throughout all traps was 227 (Day 3; Figure 5.2). 7 traps featured deer trails within the $10m^2$ scale. Deer pellet presence at the $5m^2$ was recorded at 7 traps, ranging from 1 to 4 pellet groupings. A total of 4 imagos were confirmed to have perished in traps throughout the recording period. All traps featured at least 1 caught male throughout the recording period.

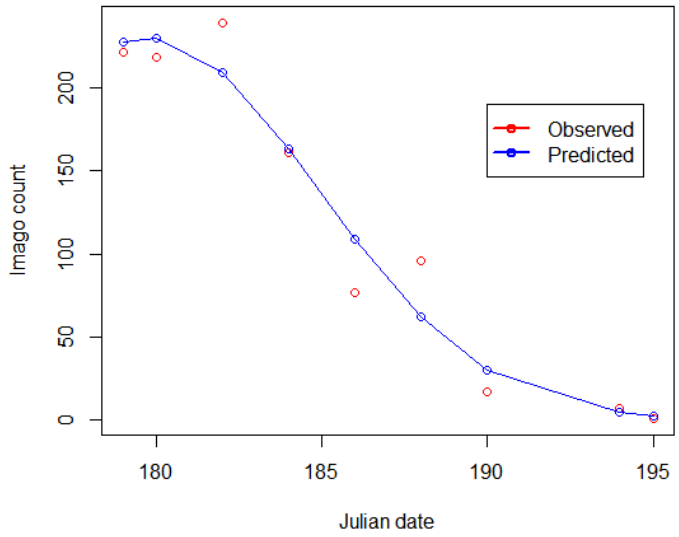


Figure 5.2. Predicted *Z. purpuralis* emergence (blue) throughout the recording season (expressed as Julian dates, e.g. Day 180 = 29/06/15) calculated from average daily trap counts (red).

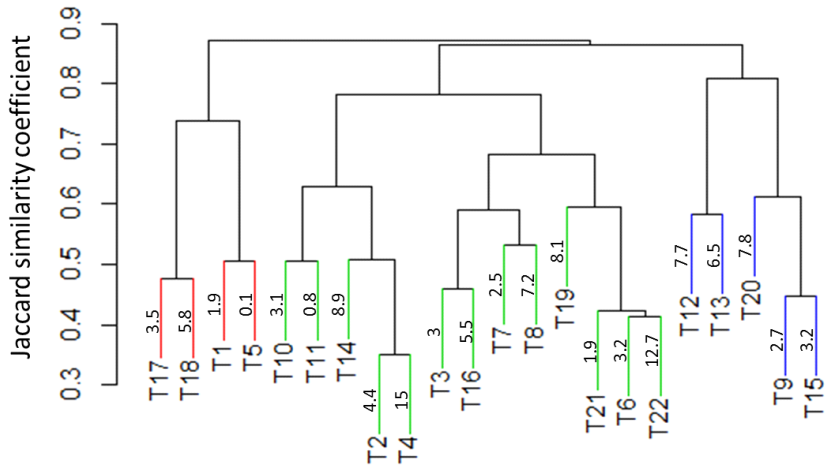


Figure 5.3. Dendogram showing trap site similarity with regards to plant species composition at the 2m scale. Sites are clustered by Jaccard similarity coefficients. Sites pertaining to one of three main divisions of species composition similarity are highlighted in red, green and blue. Site names are detailed at the bottom of each branch. Vertical values listed on terminal braches indicate the average number of *Z. purpuralis* caught at the respective trap site.

5.3.2. MICROHABITAT CONDITIONS

All trap locations occurred on coastal slopes (22-80 mamsl) below tall basalt cliff faces. All were on south, south-easterly and south-westerly facing slopes that featured a steep incline (30-40º). There were no pellets pertaining to sheep, horse, goat, cattle or goose present at any location. All traps were located to the north of the path system. All sites featured loose and unstable soil conditions, vegetated by a relatively herb-rich community relative to the other HA habitats. Vegetation height within the $2m^2$ scale ranged from 37cm to 101cm, and there was significant differences in the mean heights recorded at trap sites ($F_{21,128} = 9.46$, $P < 0.001$) (Table 5.1). *P. erecta* was the most commonly found flower, found at >20% cover at 6 sites, whereas *T. repens* was the least prevalent, found at 5% cover or less at 18 sites (Table 5.1). *H. mollis* was the most prevalent species, found on all sites, and occuring at >20% cover at 17 sites (Table 5.1). Trap 22 featured the strongest vegetation diversity with a Shannon-Weiner Index of 12.7, and Trap 5 was the least diverse at 0.1 (Figure 5.3) as characterized by 70% *H. mollis* and 11% *Fescue spp* and *Agrostis spp*. (Table 5.1). From visual inspection of the Shannon-Weiner dendogram (Figure 5.3), it can be assumed that high imago counts are not associated with any particular vegetation composition, and site diversity is not reflective of the diversity at neighboring sites.

Of the 13 different variables tested at the $2m^2$ scale, 4 were retained in the best model (Table 5.2): vegetation diversity, and the cover of heather, *H. mollis* and *T.serpyllum* ($\Delta AIC = 0$). The total number of imagos found in traps shared a positive relationship with *Thyme* cover and vegetation diversity, and was negatively influenced by heather and *H. mollis* cover (Figure 5.4 ; Table 5.2). Deer pellets were not found to be more numerous in areas of high local plant diversity ($F_{1,20}=2.164$, $P= 0.157$).

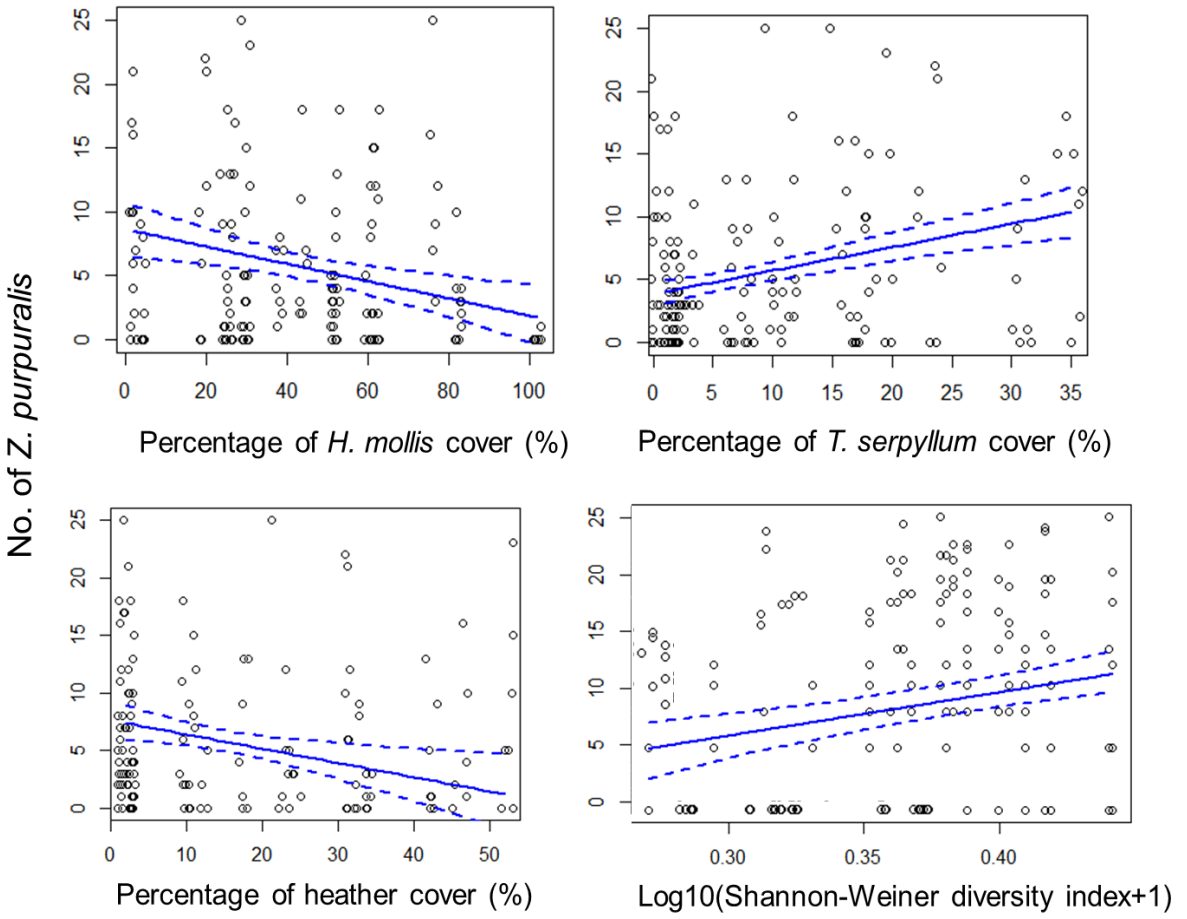


Figure 5.4. The main effects of *H. mollis* cover (top left), *T. serpyllum* cover (top right), heather cover (bottom left) and Shannon-Weiner diversity (bottom right) on the abundance of imagos at trap sites. Solid line represents the mean main prediction of the variable of interest whilst restricting all other predictors retained in the best model at mean values. Dotted lines represent confidences intervals (CIs) calculated from bootstrapping the respectice main prediction (n=1000). Data points are jittered to show overlapping values.

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Table 5.1. The average number of imagos (± SE) found at trap locations mean height (cm ± SE) and composition (% cover) of the vegetation within 2m^2 of trap locations (listed as T1-22). Only data for the major plant species tested in statistical analyses are presented. *Fescue spp*. – *Agrostis spp*. and *C. vulgaris* – *E. cineria* values represent the pooled cover of respective constituents.

Z	Average no. of moths	Average height	*L. corniculatus*	*C. vulgaris* *E. cinerea*	*Fescue spp.* *Agrostis spp.*	*T. serpyllum*	*H. mollis*	*P.erecta*	*G. verum*	*T. repens*
T1	1.89 ± 0.61	12.6 ± 1.55	7	2	11	1	52	9	0	1
T2	4.44 ± 1.89	16 ± 2.35	0	18	9	7	26	5	7	0
T3	3 ± 1.47	20.2 ± 11.35	1	12	21	1	61	7	9	5
T4	15 ± 7.59	9.2 ± 1.96	7	22	5	9	31	1	5	7
T5	0.11 ± 0.11	20 ± 4.79	1	0	11	1	70	0	0	1
T6	3.22 ± 1.75	10.2 ± 3.22	1	10	7	7	62	7	5	1
T7	2.56 ± 1.09	9.6 ± 1.49	1	2	21	1	82	1	1	3
T8	7.22 ± 1.88	8 ± 0.47	13	2	17	1	52	1	9	7
T9	2.78 ± 1.27	8.4 ± 1.29	1	32	69	7	4	9	21	1
T10	3.11 ± 1.24	11 ± 1.22	5	24	3	0	31	25	3	1
T11	0.89 ± 0.42	14.2 ± 3.47	1	34	7	1	52	33	1	1
T12	7.78 ± 4.1	9.6 ± 0.41	23	46	9	7	2	9	0	1
T13	6.56 ± 2.68	10.6 ± 0.63	1	52	11	9	31	21	1	1
T14	8.88 ± 2.99	14.2 ± 2.12	17	32	9	23	9	7	7	5
T15	3.22 ± 1.6	8.6 ± 0.63	1	42	61	31	24	21	5	0
T16	5.56 ± 1.94	11 ± 4.03	0	10	19	3	44	21	7	1

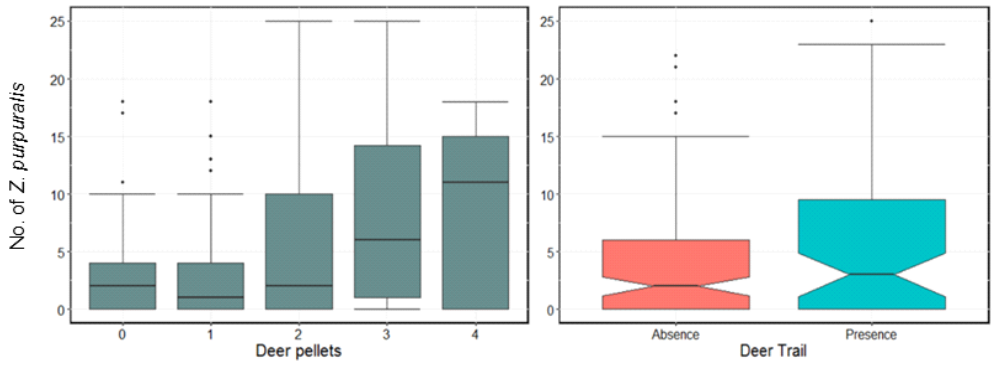

Figure 5.6. The total abundance of imagos found at trap sites in relation to the number of deer pellet groupings (left) and the presence of a deer trail within a $5m^2$.

At the $5m^2$ scale, deer pellet abundance, deer trail presence and *P. aquilinum* cover were retained in the best model (ΔAIC = 0); however, a simpler model that retained average wind-speed instead of *P.aquilinum* cover was also selected (ΔAIC = 0.44), suggesting that *P.aquilinum* cover is less influential in predicting imago abundance than pellet abundance or deer trail presence (Table 5.2). Imago abundance was positively influenced by deer pellet abundance (Figure 5.6), and significantly more imagos were found at trap sites that featured deer trails (Figure 5.6). Both average windspeed and *P. aquilinum* cover shared a negative relationship with imago abundance. *P. aquilinum* cover was also retained in the best model at the $10m^2$ scale (ΔAIC = 0) and shared a negative relationship with imago abundance (Figure 5.7). No other variables were retained at the $10m^2$ scale, and no variables were retained at the $50m^2$ scale (null ΔAIC = 0).

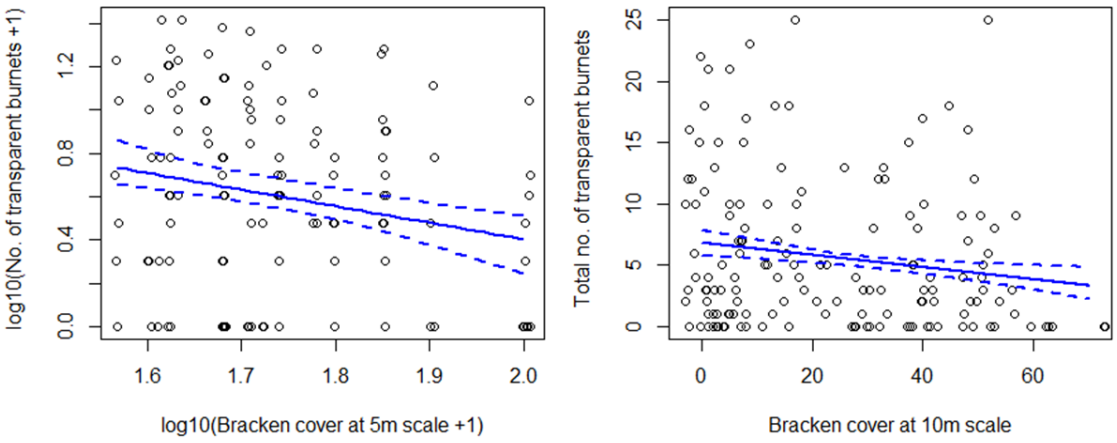

Figure 5.7. The main effects of *P. aquilinum* cover at the $5m^2$ scale (left) and at the $10m^2$ scale (right) on the abundance of imagos. Solid line represents the mean `main prediction of the variable of interest whilst restricting all other predictors retained at mean values. Dotted lines represent CIs calculated from bootstrapping the respective main prediction (n=1000). Variables were increased by the value of 1 and logarithmically transformed at the $10m^2$ scale. Data points are jittered to show overlapping values.

Table 5.2. Regression model outputs of imago abundance tested against variables at $2m^2$, $5m^2$ and $10m^2$ scales. Displayed models include all the retained models with ΔAIC<6 for each scale, whilst omitting models that represented more complex versions of retained nested models. The null model was retained for the $50m^2$ model. All models include random intercepts for recording day and site.

Scale		*AICc*	*ΔAICc*	*df*	*LL*
$2m^2$					
Model 1	SHANNON + HEATH + VGRASS + THYME	182.7	0	6	-692.787
$5m^2$					
Model 1	PELLETS + TRAIL + BRACKEN	965.2	0	5	-693.942
Model 2	PELLETS + TRAIL + WIND	965.6	0.44	5	-693.742
$10m^2$					
Model 1	BRACKEN	972.4	0	3	-699.748

† SHANNON represents Shannon-Weiner diversity index. HEATH, VGRASS, THYME and BRACKEN represent heath, velvet grass, thyme and bracken % cover, respectively. PELLETS represents pellet presence as a count variable, and TRAIL represents deer trail presence as a dichotomous categorical variable. WIND represents wind speed.

5.4. DISCUSSION

This chapter presents the first use of pheromone-baited funnel traps as an ecological monitoring tool. The results generated from this have confirmed that vegetative conditions on a multiscale level influence the catch rates of pheromone-baited funnel traps. This information was used to consider what specific habitat characteristics from a variety of scales contribute to the abundance of imagos inhabiting a given locality. With the exception of *P. aquilinum* cover acting as a deterrent at both the $5m^2$ and $10m^2$ scales, trap counts were only influenced by the vegetation conditions recorded within the $2m^2$ area. Specifically, it was found that the percentage cover of the foodplant *Thyme* was an important determinant of imago abundance at the smallest scale, but did not affect trap counts at the $5m^2$ scale, suggesting that foodplant availability is only influential when found very locally. Additionally, higher moth counts were also found in traps placed in areas of non-specific high plant diversity; the evidence suggests that no particular combination of plants was favoured by imagos. Lastly, local *C. vulgaris* and *E. cinerea*, and *H. mollis* cover was found to negatively influence trap rates. In accounting for the presence of deer activity via recording pellets and trails at trap sites, it was found that areas featuring both signs of deer activity

were associated with higher *Z. purpuralis* abundance. Trail presence and pellet counts were not found to be collinear, suggesting that the association of each with *Z. purpuralis* abundance are independent of one another.

Finally, noting the emergence patterns predicted for *Z. purpuralis*, it appears that the recording period began at peak flight season. As the sites were inspected for the first emergers every second day, then there could have been at most 2 days of unrecorded imago activity. This indicates that *Z. purpuralis* emergence is initially explosive, reaching peak population numbers within 3-4 days, after which, the population gradually decrease. The season for imagos was particular late in the year recorded (T. Prescott pers. comms.), and the explosive emergence of males may be a strategy to compensate for time lost in finding newly emerged females (Nève and Singer, 2008).

5.4.1. VEGETATIVE DRIVERS OF *Z. PURPURALIS* ABUNDANCE: A MULTI-SCALE INVESTIGATION

Z. purpuralis feed predominantly on the larval host plant, *Thyme*, but small proportions of alternative nectar sources also contribute, such as *L. corniculatus*, *P. erecta*, and *T. repens* (Bourn, 1995). This explains the association of high trap counts with *Thyme* percentage cover and overall diversity, given that the forbs listed are the major contributors to diversity in grasslands (Howe, 1994), but also explains the lack of significance found with the cover of these forbs. These factors were only relevant at the smallest scale, $2m^2$. Burnets typically exhibit limited mobility (Clausen *et al*., 2001), and upon locating an ideal forb-rich patch with ample *Thyme*, are likely to remain locally in order take advantage of these resources. Consequentially, trap sites placed in ideal conditions caught large numbers of resident moths. However, the number of blooming *Thyme* forbs at the $5m^2$ scale did not influence *Z. purpuralis* abundance. Whilst *Thyme* acts as the larval hostplant and a favoured source of nectar, it is the precise conditions in which the plant occurs that are favoured by *Z. purpuralis*. Bourn (1995) surveyed the conditions surrounding *Z. purpuralis* egg sites, and revealed that females preferred to lay egg batches on the underside of low-lying vegetation so long as the plants neighboured bare ground or were located within sheltered hollows. Furthermore, although *Thyme* was the preferred foodplant at certain sites, other plants were favoured elsewhere. Perhaps this was also true of the different trap-sites in the current study, and females were selecting from a range of favourably placed plants for oviposition, and it was not the amount

of *Thyme* but the availability of these conditions that influenced *Z. purpuralis* abundances. Alternatively, the lack of an effect may be due to the coarser method used to quantify the hostplant at this scale, and whilst more laborious, recording the percentage cover of *T.serpyllum* at the $5m^2$ may have revealed an effect.

It is not surprising that *H. mollis* influenced *Z. purpuralis* negatively; as it is a tall, obstructive gramminoid that provides little value to *Z. purpuralis*. Furthermore, *Z. purpuralis* favour low-lying, early-successional grasslands, and *H. mollis* is generally associated with grasslands of a later seral stage (Ovington, 1953). Whilst a source of nectar, *C. vulgaris* and *E. cinerea* also represent a divergence from suitable habitat, the presence of which reduces the availability of low-lying forbs and grasses in sheltered hollows in the ground.

P. aquilinum proved to be a strong deterrent of *Z. purpuralis*, acting negatively at both the $5m^2$ and $10m^2$ scales. This large fern is typical of sub-climax communities, and thus represents habitat conditions that are incongruent with the needs of *Z. purpuralis*. Since *P. aquilinum* is a negative influence of *Z. purpuralis* at the $10m^2$ scale, it is plausible that it also presents obstructive architecture to the environment, and limits the number of moths that can access a given trap. During the time that fieldwork took place, *P. aquilinum* was at peak growth, and can reach up to 1.5m in height (Marrs *et al*., 2000). As weak flyers, *Z. purpuralis* may struggle to navigate through *P. aquilinum* thicket. By limiting *Z. purpuralis* dispersal, *P. aquilinum* cover may fragment suitable habitat into isolated patches that experience limited migration, thus enforcing a metapopulation structure (Hill et al., 1996b). Unfortunately, the isolation and size of patches of grassland were not taken into account in this study, and the connectivity between patches cannot be determined. However, quantifying the distance to and number of neighbouring patches may be a more useful metric in understanding the drivers of *Z. purpuralis* abundance as opposed to the cover of grassland at a given scale.

The topsoil on the slopes was loose and unstable, and all sites featured a small portion of bare soil. Although not quantified, signs of landslide activity from heavy rain and rock-fall incidents were observed frequently throughout the slopes, and these natural occurrences potentially maintain a degree of exposed soil on these sites. The percentage of bare cover soil did not affect *Z. purpuralis* abundance directly, but may be responsible for contributing to the diverse vegetation found in these habitats (McIntyre and Lavorel, 1994).

5.4.2. IMPACTS OF DEER ACTIVITY UPON *Z. PURPURALIS*

Trails and pellet counts represent separate associations of deer activity with *Z. purpuralis* abundance. As discussed in **Chapter 4**, pellets and trails do not index the same type of habitat use; pellet presence is assumed to be a proxy for overall habitat use, whilst the formation of trails specifies the spatial nature of concentrated and repeated locomotory behaviours. The results from this study then show that *Z. purpuralis* abundance is positively associated with areas of relatively high deer use, and additionally, with the formation of deer trails.

As discussed previously, *Z. purpuralis* abundance is positively affected by plant diversity, but this effect might be indirectly influenced by deer habitat use. Ungulate grazing can either inhibit or promote plant diversity, depending upon the ability of vegetation to tolerate grazing pressures and the selectivity exhibited by the ungulate (Augustine and McNaughton, 1998). In general, where grazing is characterised by strong selective pressures due to an abundance of chemically defended or otherwise unpalatable vegetation, overall diversity is lowered due to a concentrated effort of grazing on palatable plant species (Pastor and Cohen, 1997). Conversely, in a situation where palatable plants are largely tolerant of herbivory, unpalatable plants cannot dominate the community (Augustine and McNaughton, 1998). In grassland habitats, forbs and herbs contribute to most of the species diversity (Howe, 1994). Grasses typically exhibit a stronger degree of tolerance towards grazing pressures than forbs, having evolved alongside grazers (McNaughton, 1979). Ungulates can therefore promote grassland vegetation diversity by strongly selecting graminoids over forbs. For example, *B. bison* graze almost exclusively upon graminoids, and therefore promote forb abundance by restricting the competiveness of graminoids on forbs (Knapp *et al*., 1999). On the other hand, Anderson *et al*. (2001) showed that *O. virginianus* preferred flowering forbs over grasses, and this selective grazing caused a shift in plant species abundance and competitiveness that favoured grasses over the forbs, lowering overall plant diversity. On Ulva, deer have been shown to spend more time in grasslands than other habitats on Ulva (**Chapter 4**), and these habitats are used mostly for foraging (**Chapter 3**). Therefore, trap sites with higher deer habitat use are likely experiencing a stronger degree of grazing pressure. However, the lack of a deer habitat use effect upon plant diversity provides evidence that deer are not selectively foraging forbs to the extent of lowering plant diversity. Additionally, this suggests that the association of red deer habitat use with *Z. purpuralis* abundance does not reflect a shared attraction to areas featuring rich plant diversity.

Whilst there is no evidence that deer have a negative impact on plant diversity, whether deer grazing is promoting or simply maintaining the plant diversity on these slopes is beyond the scope of this study. Alternatively, species richness may not be affected by deer habitat use or grazing pressures at all, but rather by the presence of pellets. Faecal matter is more labile than plant litter, and can significantly influence the soil properties by returning readily decomposable nutrients into the system (Van Der Wal *et al*., 2004). This input of nutrients can stimulate microbial activity in the soil, and ultimately increase plant nitrogen acquisition and growth (Hamilton and Frank, 2001). Plant diversity benefits from nutrient-rich soils as species that exhibit tolerance to poor soil conditions do not outcompete the more sensitive species (Bedford et al., 1999).

It is not surprising that deer trails are associated with high *Z. purpuralis* abundance, as deer trails provide bare soil. *Z. purpuralis*, along with related species, benefit from bare soil as the darker surface absorbs more heat than green vegetation, and complements the conditions of a warm microclimate favoured by various zygaenids (Ravenscroft and Young, 1996b). Additionally, female *Z. purpuralis* exhibit strong selectivity when laying egg batches and prefer sites close to exposed soil (Bourn, 1995). As discussed in **Chapter 4**, the formation of deer trails was caused by daily altitudinal descents/ascents, and were therefore found more frequently on sloping terrain. The slopes inhabited by *Z. purpuralis* were used by deer for this purpose and as such maintained an aspect of the microhabitat conditions necessary for the persistence of the burnet species. Moreover, *Z. purpuralis* have been recorded to benefit from trampling of mosses and grasses by livestock, as compressed vegetation retains more heat (Bourn, 1995). The diurnal migration of deer that passed through these slopes may have been similarly trampling over the vegetation and further maintaining suitable habitat for the *Z. purpuralis*.

5.4.3. NOTES ON THE UTILITY OF PHEROMONE TRAPS IN ECOLOGICAL INVESTIGATIONS

By taking into account a variety of scales, a trend of decreasing influence of vegetation with increasing scale size was revealed; trap rates were explained by multivariate processes at the $2m^2$ and $5m^2$ scales, whereas a singular variable operated at $10m^2$, and no influence was found whatsoever at the $50m^2$ scale. As discussed, this pattern can be explained sensibly by biological rationale. However, as the methods used in this study are novel, it is particularly important to consider the possible limitations

associated with this approach that may affect the results. The density of pheromones in the air likely deteriorate with increasing distance from the lures, and as such, it would become increasingly less likely for moths to detect the pheromones. In this study, wind was found to have a negative, albeit weak relationship with catch rates. It is conceivable then that this effect could be problematic at other sites that experience higher wind-speeds than the sheltered hollows inhabited by *Z. pupuralis*. After a certain distance, a threshold will be reached after which the density of pheromones is undetectably low, delineating the extent of the 'catchment area'. In this study, the catchment area of the pheromones was unknown, and so a multitude of scales were investigated. If the catchment areas was considerably less than $50m^2$ in diameter, then the entire abundance of moths within $50m^2$ was not investigated. If the dimensions of the catchment area are known, then the appropriate scale can be investigated at a suitable resolution without the loss of time and effort in researching irrelevant habitat.

When baiting funnel traps, lures were derived from female pheromones, and so only the males were caught. When used as a tool to investigate species abundances or densities, it is important to consider the potential bias that may arise from solely sampling males in the population. Gendered differences in the residence times and life expectancies of Lepidoptera have been documented previously, for example, Gall (1984) found that females lived longer and emigrated from the natal site at a much older age than males. Interestingly, this suggests that sampling from one gender of the population may be further confounded by age. For instance, male *Mellicta athalia* have been shown to exhibit a reduction in range size from 120m to 60m as they aged, whereas females movement increased from 30m to 100m with age (Warren, 1987). For *Z. purpuralis*, both sexes exhibit a range of up to 50m for the majority of the flight season, however both exhibit a distinct increase in the distances travelled after a few days (Bourn, 1995). In the current study, funnel traps were placed at 50m intervals along the band of suitable habitat underneath the basalt cliffs, and so (barring the departure from suitable habitat) any emigrating individuals were likely to have been caught in another trap. All traps rates deteriorated over the course of the flight season in a gradual and uniform manner, which suggests no trap site was biased by a local exodus. As the life histories of both genders are similar for *Z. purpuralis*, sampling males was a reliable estimate of overall population abundance. However, with respect to the utility of pheromone traps as an ecological monitoring tool, an understanding of potential sex-based differences in a species of interest should be an important prerequisite before making population-level assumptions. It is also important to note that many Lepidoptera species

exhibit sex-specific wing patterns, and Bowers *et al*. (1985) found that female *Euphydryas chalcedona* experienced higher rates of bird predation, likely as a consequence of females exhibiting stronger wing colouration. It is unlikely that this was an issue in the current study as colouration in *Z. purpuralis* does not vary with gender, but it is an important consideration for applying these methods with other Lepidoptera.

It is unclear how the presence of pheromones may disrupt emigration patterns, as artificially imposed attractants may override the behavioural stimuli to engage in natural dispersion. This could be revealed by pairing pheromone-baited funnel traps with mark-release-recapture (MRR) methods. Traps could be placed at increments from the natal site to test whether or not individuals still engaged late-season emigrations when exposed to artificial attractants. Furthermore, by identifying individuals, this method could also be used to measure the distances at which pheromones traps operate, i.e. quantify the catchment areas. The addition of MRR would therefore not only increase the potential scope of pheromone-based investigations, but also establish the limitations of these methods.

5.4.4. CONCLUSION

Whilst this study was observational in nature, there was evidence that the feeding habits and behavioural ecology of red deer may be maintaining or promoting *Z. purpuralis* habitat. Deer were found to prefer areas with higher *Z. purpuralis* abundance, which suggests that grazing is beneficial in maintaining biodiverse habitat that remains in an early-successional stage. More legitimate claims can be made with regards to the provision of bare soil through the formation of deer trails. Bare soil is a key condition for *Z. purpuralis* microhabitat, and indeed, abundances were less at sites lacking in deer trails. Whether or not the grazing patterns are in aid of the *Z. purpuralis* population, the unique diurnal migration of red deer may mean that the ungulate is a suitable grazer for maintaining the particular requirements of burnet moths.

P. aquilinum is a competitive and dominant invasive species on Ulva, and the control of which demands substantial land management (J. Howard pers. comms.). The encroachment of *P. aquilinum* upon the slopes seems to be creating a mosaic of grassland patches, threatening the persistence of the *Z. purpuralis* populations through patch isolation and habitat fragmentation. There are serious conservation implications regarding this dynamic; when isolated or in face of habitat loss, insect populations are

particularly susceptible to decline, as the rate of local extinction often exceeds that of habitat colonization (Hanski and Thomas, 1994). *Z. purpuralis* are weak flyers, and may be particularly susceptible to the problems of existing in an increasingly disjoint metapopulation structure (Franzén and Ranius, 2004).

This study has proven that pheromone-baited traps can be used to accurately investigate the ecological drivers of local *Z. purpuralis* abundance, as the results were congruent with previous studies on the species. By coupling pheromone-baited traps with MRR methods, not only could a wider range of questions regarding the ecology of a given species be answered, but some of the limitations inherent in the methodology could be addressed. The methods used in this study were relatively harmless, and pheromone-baited traps could be employed for conservation perspectives. For example, these methods are appropriate to retrieve a specimen of an endangered species from the wild, or to determine the presence of a species in degraded or restored colonies. As such, the potential uses for pheromone methods are not restricted to purely ecological perspectives, and the scope for future work is extensive.

CHAPTER 6

GENERAL DISCUSSION

‘When Death’s dark stream I ferry over

(A time that surely shall come,)

In heaven itself I’ll ask no more,

Than just a Highland welcome’

- Robert Burns

6.1. SUMMARY OF MAIN FINDINGS

This study used a variety of novel techniques to investigate the influence of disturbance stimuli upon deer behaviour and patterns of habitat use, and consequently, the ecological impacts of this relationship. These findings have added to the current knowledge of red deer behaviour, *Z. purpuralis* persistence in the UK, and furthered our understanding of disturbance ecology. New observations were revealed in each chapter by utilizing the following novel techniques: in **Chapter 3**, thermal imaging equipment was used to investigate hitherto unstudied nocturnal behaviour in free-ranging red deer, and zero-one inflated beta regression models were used to appropriately analyse the data; in **Chapter 4**, camera traps were used to quantify the overlap of path use between tourists and red deer; and finally in **Chapter 5**, the specific habitat requirements for *Z. purpuralis* were uncovered through the original design of combining pheromone-baited funnel trap methods with traditional ecological surveying methods. Furthermore, **Chapter 5** also provided the first evidence that deer are contributing to the persistence of *Z. purpuralis* via the provision of bare soil in the form of deer trails.

The most important discovery of this thesis comes from the synthesis of the findings from **Chapters 3-5 –** linking the variability of deer behaviour and patterns of habitat use in response to different levels of anthropogenic disturbance to the persistence of *Z. purpuralis*. It is widely documented that grazing can affect invertebrates and plant species by directly modifying the physical structure and plant composition of the habitats (Baines *et al*., 1994, Burger *et al*., 2000, Clarke *et al*., 1995a, Clarke *et al*., 1995b, Colquhoun, 1970, Feber *et al*., 2001, Hester *et al*., 1996, Hobbs, 2009, Kruess and Tscharntke, 2002, Melis *et al*., 2006). However, this study has provided the first insights into the cascading effects of disturbance stimuli upon habitat management via the alteration of the behaviour and habitat use of a key grazer. Specifically, when experiencing higher levels of human activity in the IB, deer exhibit habituation by reducing the amount of time spent in anti-predator behaviours and by occupying areas associated with human activity. However, in areas with relatively low amounts of human activity, deer routinely disrupt foraging bouts by engaging in anti-predatory behaviours and avoid areas associated with human presence. By controlling these patterns of habitat use and foraging behaviours of red deer, human presence can indirectly dictate the grazing regime experienced in certain habitats. In the case presented in this thesis, the population of *Z. purpuralis* on the southern slopes of the HA benefit from the behavioural patterns of

deer adopted in response to the levels of tourist activity in the area. Furthermore, this thesis has proven that red deer are a viable grazing tool for land management schemes.

6.1.1. DOES INCREASED ANTHROPOGENIC DISTURBANCE RESULT IN HABITUATION?

As stated, deer in the HA dedicated more time towards anti-predator behaviours, and favoured areas with increasing distance from the path. Whilst deer in the IB were somewhat sensitive to path traffic and tourist season, head-up behaviours in response to path proximity was markedly reduced. Moreover, no area in the IB was favoured with regards to path proximity. The restricted use of areas associated with human presence in the HA is a reliable indicator that deer are perceiving human activity similarly to predation risk. Creel *et al*. (2005) found that red deer similarly avoid certain areas associated with wolf presence, and spent less time in open grassland habitats. Furthermore, both bison and red deer have been shown to reduce foraging behaviours in favour of performing anti-predatory scanning behaviours in areas inhabited with wolves (Laundré *et al*., 2001). From this, it seems that deer in the IB have developed a degree of habituation towards frequent tourist presence. Conversely, human disturbance is less recurrent in the HA and is perceived by deer to be analogous with true-predation risk, owing to the similar modifications in scanning times and habitat use shown in response to the presence of true predators (Creel *et al*., 2005, Kamler *et al*., 2007, Laundré *et al*., 2001).

Foundational to the aims set out in **Chapter 3 and 4**, red deer were assumed to form two distinct populations, residing in the HA and the IB, respectively, and were compared in terms of behaviour and habitat use. Inferences regarding levels of habituation were made under this assumption, leading to the argument that deer residing in the IB are better adapted to tolerate human activity than deer in the HA. This argument was extended to support the idea that the 'risk-disturbance' effect is reduced when human disturbances are frequent, as IB deer are exposed to more disturbance over time and now dissociate human presence from true predation risk.

The degree, if any, of migration between the two sites is unknown. Certainly, there are qualitative records of deer swimming from Mull to Ulva, and individual deer have been recorded in both sites (J. Howard pers. comms.). If the migration is low, then the results of this study represent the behaviour of residential deer that are adapted to the conditions of a given site. However, if migration is occurring frequently, then the patterns in time budgets and habitat-use recorded reflect the behaviour of visitor deer.

In such a situation, differences in the behaviour between the two sites would suggest that red deer exhibit strong behavioural plasticity, and are capable of rapidly altering responses to the levels of disturbance in a new environment. There is evidence that the 'risk-disturbance' hypothesis is temporal in nature, whereby wildlife dissociate human disturbance from predation risk during important life history stages (Peters and Otis, 2005). Perhaps there is also a spatial component to the risk-disturbance hypothesis, and human presence is only perceived to be analogous to predation risk in certain environments. If true, the implications from this dynamic would define the development of habituation in the IB deer within a proximate framework (behavioural plasticity), rather than from an ultimate perspective (learned behaviours).

6.1.2. THE ROLE OF DEER IN MAINTAINING BIODIVERSE SHORT-SWARD HABITATS

The efficacy of using deer for conservation grazing as opposed to sheep is grounded on two arguments: first, differences in the general behaviour and grazing ecology of the two ungulates; and second, by the inherent fact that wild red deer are susceptible to displacement by human presence. The differences in the grazing habits between the two species has been covered in depth (Clarke *et al*., 1995a, Clarke *et al*., 1995b, Colquhoun, 1970, Hester *et al*., 1996, Hester and Baillie, 1998, Milne *et al*., 1978), and so one of the main over-arching themes of this thesis was to investigate the latter argument. As reasoned, deer in the HA seem to perceive tourist disturbance as analogous to predation risk with respect to time budgets and habitat use. This is an important component of red deer behaviour that allows the species to act as an effective grazing tool in maintaining biodiverse grasslands as human presence causes deer to terminate foraging bouts in order to engage in anti-predatory behaviours. Moreover, grasslands located in areas close to human activity are used less. Consequently, the grasslands are kept at an early-intermediate seral stage that benefits the burnet moth species found on Ulva. Few studies have quantified the effects of path traffic volume on ungulate habitat use and behaviour (Pelletier, 2014), yet it was an important consideration in the current study. The path system closest to the short-sward habitats was seldom used by tourists, and since deer dedicated less time to vigilance and more time feeding if the closest path experienced low traffic, it is probable that deer were seldom disrupted from feeding and kept the grassland from becoming too rank. However, unlike the deer in the IB, disturbance was not so frequent that HA deer resumed foraging times regardless of tourist traffic or distance to the nearest path. This lack of habituation

may be an important factor for maintaining these grasslands. As disruptions in the foraging bouts may be necessary in preventing the short-sward grasslands from becoming over-grazed, and it could be argued that these habitats are benefitting from a subtle blend of low but present tourist activity in the area. As the deer in the IB seem to be more habituated to human presence, habitats may experience a greater intensity of grazing due to the relatively low amounts of time invested in head-up behaviours in comparison to deer in the HA. Lepidoptera that favour much earlier-successional grasslands than those favoured by burnet moth species, such as the *E. aurinia* (Hula *et al*., 2004), may benefit from this regime in the IB.

Lepidoptera undergo profound changes throughout each stage of the life history (egg, larva, chrysalis, imago), and the habitat requirements for each stage can be drastically different from one another (Stewart, 2001). *Z. purpuralis* exhibits limited dispersal abilities, and so the range of habitat conditions required for each life history stage needs to be met within a relatively localised area (Tremewan, 1985). Regarding this, an appropriate grazer needs to maintain or promote small-scale heterogeneity in plant species composition and habitat structure. Deer have been suggested to be an appropriate grazer in maintaining this type of biodiverse mosaic-like habitat structure, as they alternate between browsing on heather and grazing on ground vegetation. (Stewart, 2001). Conversely, sheep are principal grazers, and seldom take from heather or other shrubs (Colquhoun, 1970). Indeed, an enclosure experiment showed that red deer foraged on heather for approximately 40% of the total time spent foraging, compared to 9% for sheep (Clarke *et al*., 1995a). As such, it is entirely plausible that the light deer grazing on the ground flora with intermittent heather browsing is encouraging forb-rich *Z. purpuralis* habitat. This is supported by the results presented in **Chapter 5**, as deer presence was found to share a direct positive relationship with the Shannon Weiner diversity at trap sites. Indeed, it has been previously documented that by arresting the succession of grassland habitats, deer grazing can be highly beneficial for thermophilous invertebrates that require flowers for pollen and nectar (Stewart, 2001), much like *Z. purpuralis.*

Deer may additionally distribute nutrients sporadically throughout the feeding areas by removing material from one area through feeding, and depositing them elsewhere through defecation (Stewart, 2001). This is more prevalent in wild ungulates than domestic livestock, as intervals of walking between foraging behaviours are more frequent, possibly to avoid the vulnerability associated with spending too much time feeding in a predictable manner (Godvik *et al*., 2009, Ruckstuhl and Neuhaus, 2000). This

could explain the positive *Z. purpuralis* abundance with the direct presence of pellets, as opposed to assuming that *Z. purpuralis* abundance is positively correlated with habitat use.

6.2. JUSTIFICATION OF METHODOLOGY AND FUTURE RESEARCH

Traditionally, methods used to sample Lepidoptera either use the Pollard Yates technique, or similar procedures that involve observers patrolling along transects (Pollard, 1977, Thomas, 1983, van Swaay *et al*., 2008). Pheromone-baited traps also allow for the sampling of a given population, from which abundance, density or simple presence/absence data can be retrieved. However, the chief difference is that a specific species is attracted to funnel traps, whereas in traditional methods single or multiple species are located and identified via observers. Therefore, pheromone-baited trapping samples a given population in much the same way that baited pitfall traps and snap-and-live traps sample small mammal populations (Williams and Braun, 1983), or how catnip-baited glue traps can be used to attract and collect fur from individuals in a population for genetic analysis (Mowat and Paetkau, 2002). These techniques are often employed to study wildlife that is elusive in nature or exists at sparse densities, such as felines (Animal and Use, 1998), or those that are impractical or unreliable to observe in the field, such as small insectivores or rodents (Williams and Braun, 1983).

As such, pheromone-baited trapping is subject to similar bias inherent in other 'attractant' methods found in ecology (Smith *et al*., 1975). With small mammal trapping for example, all types of trap will capture sexes and age-classes at different probabilities, resulting in an untrue representation of the population sampled (Williams and Braun, 1983). Similarly, the pheromone-baited funnel trapping design used in this thesis solely sampled males. Consequently, it could be argued that caught specimens primarily represent a later age-class, as older males were more likely to migrate to greater distances and therefore encounter funnel traps (Bourn, 1995). Wing condition, a metric used to determine age in Lepidoptera, was not recorded, and so it is unknown whether pheromone traps were sampling the older individuals from the population. These are important details, and a true subsample of the population cannot be attained from the pheromone-trapping methods detailed in **Chapter 5**. However, as the aim was to relate overall abundance to habitat conditions and deer presence, the only assumption underlying these

methods was that male imagos would represent the habitat preferences of *Z. purpuralis* as a species in general. Since the habitat preferences of *Z. purpuralis* are not known to be gender-specific (Bourn, 1995), the abundance of caught males in relation to local habitat conditions is likely to correlate with the total population abundance in the same area, rendering these confounding factors somewhat irrelevant.

In this thesis, deer behaviour and habitat use were measured via direct observations and indirect faecal recording, respectively. This design provided key information about the general behaviour of deer and habitat use in biodiverse grassland areas. Whilst these methods were sufficient in addressing the aims of this thesis, the investigation was conducted at a broad scale; behavioural observations were limited to examining differences in overall time budgets and patterns in habitat use were captured at the seasonal scale. Therefore, the behavioural and habitat use patterns that operate at a finer scale are still unknown.

Investigating foraging behaviour at a finer resolution may reveal important implications for maintaining the biodiverse grasslands in the HA. Feeding intensity can be investigated via bite rates, which have been shown to increase in ungulates when exposed to a greater density of conspecific and heterospecific grazers (Ferretti *et al*., 2015). The absence of livestock for most of the year in the HA may have significance in achieving suitably high grazing pressures for maintaining the early successional grasslands needed for *Z. purpuralis* and *Z. loti*. By comparing the bite rates of red deer between the HA (low livestock presence) and IB site (high livestock presence), the importance of competition between herbivores in maintaining early-successional grasslands could be investigated.

Remote monitoring of wild animal activity is becoming increasingly available for ecologists as recent technological advances have allowed for sensors such as cameras, GPS, magnetometers, heart rate monitors and accelerometers to be fitted into lightweight animal-borne devices (Butler and Jones, 1997, Recio *et al*., 2010, Suzuki *et al*., 2009, Williams *et al*., 2014). These devices can be used to remotely measure the aspects of physiology, behaviour, movement patterns and community interactions in free-ranging wildlife (Wilmers *et al*., 2015). Sensors can be used in conjunction to increase the scope of investigation. For example, camera devices fitted to free-ranging Adélie penguins (*Pygoscelis adeliae*) allowed for prey identification, whilst simultaneous accelerometer data verified the success of prey capture, ultimately allowing researchers to determine the respective capture success of the different prey species taken by Adélie penguins (Watanabe and Takahashi, 2013).

Tri-axial accelerometers are activated by animal movement. These sensors continuously record tri-axial motion values and when placed on the neck of an ungulate (e.g. on a collar), they are sensitive to vertical and lateral head movements, and the speed at which movements are made (Adrados et al., 2003a). These motion values correspond to an engaged activity of a given animal, and by simultaneously observing behaviour whilst recording accelerometer data, behaviours can be discriminated remotely via accelerometer values (Löttker *et al*., 2009). Therefore, in conjunction with GPS technology built into the collars, key behaviours can potentially be mapped (Cagnacci *et al*., 2010). If applied to the deer of Ulva, this approach could reveal the fine-scale habitat selection patterns within seasons, between week-days and weekends, and throughout the nychthemeron.

The exact nature of behavioural responses following tourist encounters were not investigated, nor was any subsequent change in habitat use. The degree to which wildlife is displaced following a tourist encounter is dependent on levels of habituation (Newsome *et al*., 2005). Given that deer residing in the IB exhibit relative habituation, it is conceivable that tourist-related displacement effects will be short-lived, and consequently, the grassland communities will not experience a decrease in levels of grazing. By experimentally disturbing GPS collared deer, the severity of displacement and subsequent compensatory feeding could be compared between sites. From this, how future changes in tourist numbers on Ulva may impact upon the grazing regimes of deer could be predicted. Furthermore, it would be possible to reveal the behaviours of individuals in locations that were inaccessible to the method of observational recording employed for this thesis. Finally, GPS collars could also determine the degree of migration between sites, and therefore evaluate whether the behavioural differences between the two populations stems from behavioural plasticity exhibited by deer that roam both sites, or whether both populations are strongly isolated and the observed behavioural differences reflect habituation to disturbance over time.

As discussed in **Chapter 5**, *Z. purpuralis* may be benefitting from both deer grazing pressures and the formation of trails. However, the advantages of deer presence on these grassland slopes may be threefold. By removing taller vegetation, deer grazing can increase the exposure of the field layer in grasslands to the sunlight (Stewart, 2001), causing a consequential increase in temperature. Whilst this modification is documented to be harmful for certain invertebrates that depend upon humid and moist conditions (Fry and Lonsdale, 1991), *Z. purpuralis* could benefit from the promotion of these warm microclimates. To test if deer grazing induces thermal changes upon the plant community, the habitat plot

design used in Chapter 4 could be developed through the inclusion of an additional variable. Thermocouples could be placed 2mm below the soil surface to record surface soil temperatures (Franco and Nobel, 1989). To avoid differences in the structure of the microhabitats found throughout Ulva from influencing results and focus the investigation towards the promotion of *Z. purpuralis*, data collection would be restricted to the south-facing grassland slopes in the HA.

Pellet counts have been criticised on the grounds that differences in pellet presence between areas may simply reflect differences in the defecation rates for different behaviours (Anderson, 2003). Rowland *et al*. (1984) and Loft and Kie (1988) argue that supplementary information on the behaviours exhibited by wildlife in different habitats is necessary in order to make inferences about habitat use from pellet-group count data. This thesis employed a combination of behavioural observations and pellet-count surveys in order to avoid these errors and investigate the behaviours exhibited by deer in different areas and the relative use of these areas throughout the study site.

The novelty of the research presented in **Chapter 5** is twofold: first, the methodological applications of pheromone-baited traps in ecological research was introduced; and secondly, no research to date has investigated the relationship of red deer in promoting the habitat conditions required for Z. purpuralis through the provision of bare soil in the form of deer trails. As this thesis acts as the initial investigation on these topics, the scope for further research is extensive.

P. aquilinum cover had a negative relationship with *Z. purpuralis* abundance at intermediate scales, in which no positive habitat associations were found. From this, it was argued that *P. aquilinum* may act as a physical barrier to *Z. purpuralis* movement, thus limiting the catch rate of males from the wider area, regardless of whether they originated from high quality sites or not. Regarding this supposition, a more relevant way of testing important factors for *Z. purpuralis* abundance at the larger scales would be to focus on patch dynamics. Patch dynamics has been found to be an important determinant for the presence of other Lepidoptera species (Dennis and Eales, 1997, Fowles and Smith, 2006). Specifically, the number of Lepidoptera that a patch can accommodate is related to patch size, proximity to other patches, and the number of patches nearby (Hill et al., 1996a), and these factors are equally as important as habitat quality in explaining Lepidoptera incidence (Dennis and Eales, 1997). In the case of *Z. purpuralis* on Ulva, a measure of '*P. aquilinum*-enclosure' that reflects the degree of separation of a patch from the surrounding grassland may better explain *Z. purpuralis* abundances.

Z. loti similarly requires the presence of bare soil, and this is an important component of the microhabitat favoured by the species (Ravenscroft and Young, 1996a). Therefore, *Z. loti* may benefit from the presence of deer trails on these slopes. This species exhibits an even more restricted distribution in Britain than *Z. purpuralis* (Tremewan, 1985), and as such, is in greater danger of extirpation from the area. Therefore, this species merits similar attention. A *Z. loti* pheromone is currently being developed (Burman *et al*., 2014), after which, the methods employed in **Chapter 5** could be repeated for this species in order to investigate if deer are beneficially modifying favourable habitat *Z. loti*.

Whilst the observational nature of this study cannot support comment upon the relationship between *Z. purpuralis* and red deer activity beyond positive correlation, exclusion experiments could be employed to determine whether the relationship between red deer grazing directly predicts *Z. purpuralis* abundance. Exclusion methods are used extensively to test the influences of ungulate-herbivory on the community composition of ground vegetation, and the consequent indirect impacts upon associated invertebrate communities (Baines *et al*., 1994, Cooke, 1997, Russell *et al*., 2001). However, whether these impacts are negative or positive depends largely on the vegetation and invertebrates in question (Stewart, 2001). In an exclosure study conducted by Baines *et al*. (1994), it was found that red deer grazing reduced bilberry vegetation by 50%, which in turn lead to an astounding 400% decrease of geometrid larval abundance found. As most of the bilberry taken by deer composed of fresh shoots which the geometrid larvae also prefer, the deer could be acting in direct competition with the larvae for food. Additionally, in these circumstances, deer may be indirectly predating on the larvae found on the fresh tips, which may account for some of the discrepancy found between the reductions measured in bilberry and larval abundance (Baines *et al*., 1994). Such findings suggest that red deer may lack a degree of selectivity when feeding, which could be potentially dangerous for Lepidoptera species which share a preference in food-plants with red deer. Conversely, certain invertebrate species have been found at lower abundances in exclosure plots (González-Megías *et al*., 2004, Melis *et al*., 2006). For example, Suominen *et al*. (2003) found that carabid abundances were significantly higher in plots that experienced red deer grazing than corresponding un-grazed plots. Such exclosure methods could be used to ascertain whether the relationship between deer and *Z. purpuralis* found in this study simply reflects a mutual attraction to the same vegetative conditions, or if deer grazing actively promotes the abundance of *Z. purpuralis*.

On Ulva, fenced exclusion plots could be constructed on the early-successional biotopes inhabited by *Z. purpuralis*, and paired with corresponding unfenced 'reference' plots. The succession of vegetation within the plots could then be measured annually, and compared to the reference plots that are open to deer grazing. Additionally, if the same protocol was repeated for a similar site that featured sheep in place of deer, then the role of deer in maintaining these habitats could be compared with more traditional livestock used in the region.

6.3. CONCLUSIONS

In conclusion, this thesis has substantially added to disturbance ecology, habitat management ecology, and behavioural ecology by providing an important insight into the role of wild ungulates as conservation grazers. Specifically, it has revealed that disturbance stimuli can have cascading ecological effects that reach plant and invertebrate communities through the alteration of grazer behaviour and habitat use. Additionally, novel techniques were used to show that a wild ungulate can be used as an appropriate grazing tool in maintaining biodiverse grassland habitats. Furthermore, the implications of this dynamic in a conservation and management perspective have been discussed. One of the main aims of the new management scheme on Ulva was to marry biodiversity management with tourist activity, and the results of this thesis largely suggest that this is a successful strategy. However, it is realised that this dynamic may only be successful due to the conditions of Ulva, and success is dependent on several factors: the density of red deer; the disturbance regime and frequency of tourists; and the specific conservation criteria for the short-sward grasslands. Other systems may require substantially different levels of the first two components in order to appropriately deliver the third. In revealing the applicability of red deer as a conservation grazer, this thesis should initiate discussion into the use of wild ungulates as the principal grazers in other land management schemes. Future research into the applicability of such a system for other sites would undoubtedly benefit from fine-scale spatial and temporal data acquired via animal-borne sensing technology. This would also reveal the behavioural plasticity and variability of a given grazer with respect to changing levels of disturbance throughout the environment and season. However, it must be acknowledged that inferences gained from this type of methodology are typically informed from small sample sizes, as collaring a large portion of a population is impractical and expensive.

The indirect knock-on effects of tourist disturbance on habitat conditions revealed here should not be viewed solely within a nature-based management setting, however, and the findings of this thesis have far-reaching implications. Whilst the demand for nature-based tourism is increasing (McNeely, 1992), so is access to the countryside and overall human infrastructure, and consequently, wildlife is increasingly experiencing exposure to human activity (Nellemann et al., 2000b). In the case of grazers, increased exposure to disturbance could alter the grazing regimes that have been naturally maintaining biodiverse or characteristic habitats, harming the role of these grazers as natural ecosystem engineers, leading to unforeseen biodiversity loss in the form of plant and invertebrate communities. Currently, disturbance research mainly focuses on the impacts upon biology and physiology of the disturbed species (Kerlinger *et al*., 2013, Marzano and Dandy, 2012, Russell *et al*., 2009). However, as the findings of this thesis suggest, the persistence of biodiverse habitats can be reliant on delicate ecological balances, and future research should concentrate on how disturbance stimuli may erode these fragile relationships that maintain biodiversity. Whereas the key players to biodiversity loss are readily recognised in the forms of habitat destruction, infrastructure development and climate change, we need to consider the more pervasive and obscure threats that humans pose to biodiversity.

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APPENDIX

A3.1. CHAPTER 3

A3.1.1. ZERO-ONE BETA BINOMIAL MODELLING FOR FOCAL ANALYSIS

The beta distribution can be used to model continuous proportion data bounded by (0, 1) (Swearingen *et al*., 2012). The beta distribution of a beta-distributed random variable, y, incorporates the following parameters: the distribution mean *p*; and, which is a dispersion parameter for additional binomial variability, and has the following probability density function

$$P_b(y; p, \theta) = \frac{\Gamma(\theta)}{\Gamma(p\theta)\Gamma[(1-p)\theta]} y^{p\theta-1}(1-y)^{(1-p)\theta-1}, y \in (0,1), \quad (1)$$

where Γ is the complete gamma function. The mean of *y*, *E*, and its variance, *Var*, can be expressed as the following:

$$E[y] = p \quad (2)$$

$$Var[y] = \frac{p(1-p)}{\theta+1} \quad (3)$$

As the beta distribution is limited in modelling extreme observations occurring at 0 or 1, zero-one inflated beta regression is formed from a mixture of the aforementioned beta distribution with an additional discrete Bernoulli distribution to capture the probability mass occurring at 0 and/or 1 (Scott-Hayward *et al*., 2014). The probability density function of the response variable *y* is given by

$$beinf_c(y; \alpha, p, \theta) = \begin{cases} \alpha, & if\ y = c, \\ (1-\alpha)f(y; p, \theta), & if\ y \in (0,1), \end{cases} \quad (4)$$

where *f (y; p, θ)* is the beta density (2). The probability of both discrete models observing 0 (c=0) and 1 (c=1) are denoted by *α*. The mean of *y*, *E*, and its variance, *Var*, can be expressed as the following:

$$E(y) = \alpha c + (1-\alpha)p, \quad (6)$$

$$Var(y) = (1-\alpha)\frac{p(1-p)}{\theta+1} + \alpha(1-\alpha)(c-p)^2. \quad (7)$$

A3.1.2. MISCELLANEOUS EFFECTS ON INDIVIDUAL BEHAVIOUR IN THE HA

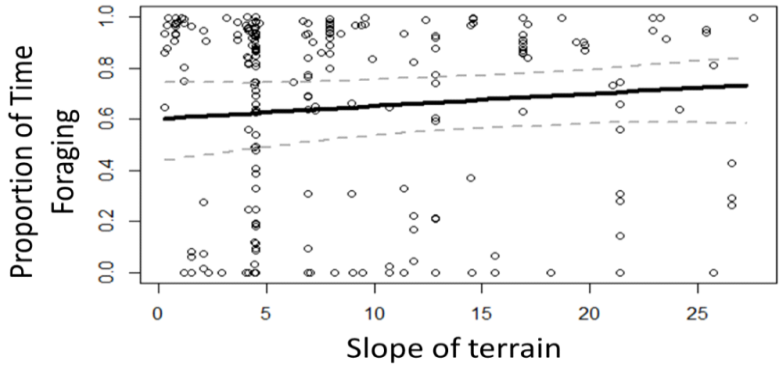

Figure A3.1. Main effects of herd size acting upon the proportion of time engaged in foraging behaviour recorded in the HA. Solid line represents the mean main prediction of the predictor of interest whilst holding all other variables retained in the model at respective means. Dotted lines represent 95% CIs. Points represent jittered observations. Results are generated from the full dataset.

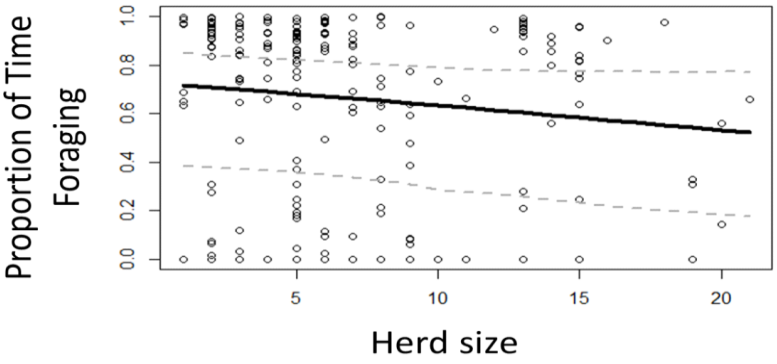

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Figure A3.2. Main effects of herd size acting upon the proportion of time engaged in foraging behaviour recorded in the HA. Solid line represents the mean main prediction of the predictor of interest whilst holding all other variables retained in the model at respective means. Dotted lines represent 95% CIs. Points represent jittered observations. Results are generated from the full dataset.

Herd size was retained in the model investigating foraging behaviour, whereby the probability of observing deer engaged in foraging behaviour decreased with increase herd size (see Figure A3.2). No predictors were retained when testing ruminating, resting, head-raised or active behaviours. Slope was retained as a predictor in explaining foraging behaviour, whereby the time spent foraging

increased with increasing steepness of terrain**.** Season was retained in the model investigating locomotion behaviours, whereby deer spent significantly more time engaged in locomotion behaviours during the tourist season than the non-tourist season.

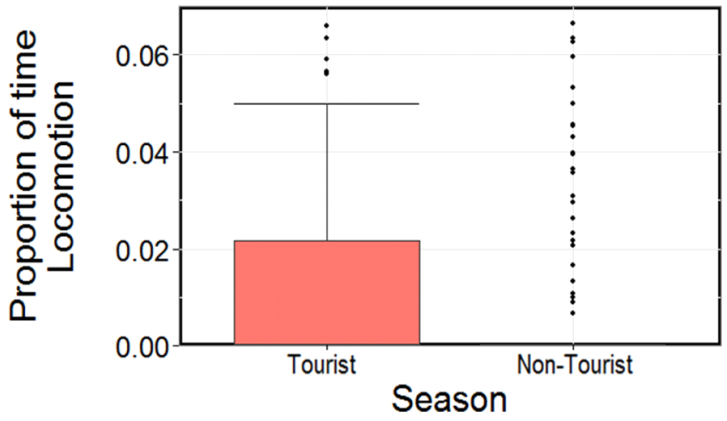

Figure A3.3. Main effect of season on the proportion of time engaged in locomotion behaviours in the HA. Boxes represent the interquartile range around the median (dark line). Whiskers represent the 75th and 25th percentile respectively. Circles outside of whiskers represent possible outliers. Results are generated from the full dataset.

Table A3.1. Activity budgets for individual red deer calculated for both HA and IB sites at tourist season (HAT, IBT, respectively) and non-tourist season (HANT, IBNT, respectively) and both seasons combined for each site (HA, IB). Figures listed are the mean percentage times spent in a given behaviour (±SE) averaged across the total number of focals (N) from the given site and season.

Behaviour	HAT (N=275)	HANT (N=194)	HA (N=469)	IBT (N=478)	IBNT (N=72)	IB (N=550)
Foraging	0.274 (0.23)	0.312 (0.031)	0.29 (0.019)	0.369 (0.018)	0.351 (0.051)	0.367 (0.017)
Rest	0.59 (0.028)	0.648 (0.034)	0.614 (0.022)	0.49 (0.022)	0.546 (0.058)	0.497 (0.02)
Walking	0.039 (0.006)	0.015 (0.003)	0.029 (0.004)	0.036 (0.004)	0.039 (0.011)	0.037 (0.004)
Ruminating	0.064 (0.02)	0.018 (0.003)	0.045 (0.006)	0.075 (0.007)	0.041 (0.014)	0.07 (0.006)
Alert	0.019 (0.005)	0.002 (0.001)	0.012 (0.003)	0.018 (0.003)	0.021 (0.009)	0.018 (0.003)
Running	0.003 (0.001)	0 (0)	0.002 (0.001)	0.003 (0.001)	0 (0)	0.003 (0.001)
Head-up [a]	0.066 (0.01)	0.017 (0.004)	0.046 (0.006)	0.132 (0.01)	0.1 (0.025)	0.128 (0.009)
Active [b]	0.340 (0.026	0.330 (0.032)	0.336 (0.020)	0.503 (0.022)	0.451 (0.058)	0.496 (0.02)
Locomotion [c]	0.042 (0.007)	0.015 (0.003)	0.031 (0.004)	0.04 (0.04)	0.039 (0.011)	0.039 (0.004)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running; [c] Locomotion = Walking + Running

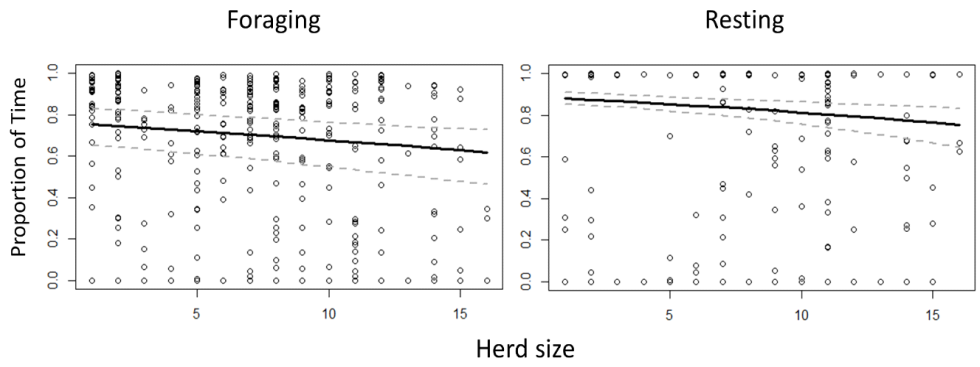

Figure A3.6. Main effects of herd size acting upon the proportion of time engaged in foraging behaviour recorded in the IB. Solid line represents the mean main prediction of the predictor of interest calculated from 1000 bootstraps whilst holding all other variables retained in the model at respective means. The area between the dotted lines represents 95% CIs. Points represent jittered observations.

A3.1.3. BETA BINOMIAL MODELLING FOR SCAN ANALYSIS

A generalized beta-binomial model was applied to the data to estimate the probability of the herd exhibiting one of the observed behaviours.

The probability mass function of the beta-binomial distribution describing the number of successes (0 ≤ y ≤ n) can be expressed as the following

$$P_{bb}(Y = y|n, p, \theta) = \frac{\Gamma(\theta)}{\Gamma(p\theta)\Gamma[(1-p)\theta]}\binom{n}{y}\frac{\Gamma(y + p\theta)\Gamma[n - y + (1-p)\theta}{\Gamma(n + \theta)}. \quad (1)$$

The number of trials is expressed by *n* and *Y* refers to a given random variable, the value of which is denoted by *y*. The distribution mean is given by *p*, whilst θ is a dispersion parameter that allows for additional binomial variability. Γ is the complete gamma function. The mean expected value (*E*) of the distribution is

$$E[y] = np, \quad (2)$$

whilst the variance (*Var*) can be expressed as

$$Var[y] = np(1-p)\left(1 + \frac{n-1}{\theta + 1}\right). \quad (3)$$

As the AIC model selection process involves likelihoods, the natural logarithm of the beta-binomial probability mass function was used in order to avoid computation of infinitely small values. Similarly with the focal analysis, HA and IB datasets were analysed separately. Predictor variables included herd size and distance to the path. Final models were selected following the Akaike's information

criterion (AIC) approach to minimizing models (Richards, 2008), whereby all models ≤Δ6 AIC are inspected, and the most parsimonious models with the lowest ΔAIC are retained, in addition to considering models that do not represent more complex versions of simpler nested counterpart models. Beta binomial regressions were modelled in R 2.15.3.

A3.1.4. DESCRIPTIVE STATISTICS GENERATED FROM SCAN SAMPLING

The total number of scans recorded in the HA and IB was 614 and 543, respectively (total=1157). All behaviours were recorded in the scan observations with the exception of 'running'. Disregarding pooled behavioural categories, on average, foraging behaviour was recorded to be exhibited by the largest proportions of the herds observed in both the HA and the IB (mean proportional times = 0.57±0.017 and 0.612±0.016, respectively), whilst vigilance behaviour was displayed by the smallest proportion of the herds observed (0.037±0.004; Table 3.7).

A3.1.5. INVESTIGATING THE EFFECTS OF PATH1 IN THE HILL AREA

With regards to the PATH1 analysis, both herd size and distance to the nearest path were not retained as significant predictors in the models investigating the probability of alert behaviours exhibited by observed herds ($\Delta AIC_{null} = 0$; Table 3.8). Herd size was retained as the sole significant predictor in the models investigating foraging ($\Delta AIC_{herd} = 0$, $\Delta AIC_{null} = 25.3$), active ($\Delta AIC_{herd} = 0$, $\Delta AIC_{null} = 29.1$), and locomotion behaviours ($\Delta AIC_{herd} = 0$, $\Delta AIC_{null} = 6.7$). Specifically, the probability of all three behaviours being observed decreases with increasing herd size (Table 3.8).

Table A3.2. Proportion of red deer herds engaged in different behaviours for both HA and IB sites calculated during the tourist season (HAT, IBT, respectively) and the non-tourist season (HANT, IBNT). Figures listed are the mean proportions observed in a given behaviour (±SE) averaged across the total number of scans (N) respective to the appropriate site and season combination. Running was never recorded in a scan.

Behaviour	HAT (N=379)	HANT (N=235)	HA (N=614)	IBT (N=487)	IBNT (N=56)	IB (N=543)
Foraging	0.468 (0.021)	0.623 (0.028)	0.527 (0.017)	0.628 (0.016)	0.479 (0.062)	0.612 (0.016)
Rest	0.33 (0.021)	0.257 (0.027)	0.302 (0.017)	0.191 (0.015)	0.402 (0.063)	0.212 (0.015)
Walking	0.075 (0.011)	0.064 (0.012)	0.071 (0.008)	0.063 (0.007)	0.007 (0.007)	0.057 (0.007)
Ruminating	0.102 (0.011)	0.045 (0.012)	0.08 (0.008)	0.084 (0.009)	0.065 (0.031)	0.082 (0.008)
Alert	0.053 (0.009)	0.01 (0.06)	0.036 (0.006)	0.036 (0.006)	0.046 (0.026)	0.037 (0.006)
Head up [a]	0.23 (0.019)	0.119 (0.018)	0.187 (0.014)	0.183 (0.012)	0.119 (0.4)	0.176 (0.012)
Active [b]	0.698 (0.023)	0.742 (0.027)	0.714 (0.017)	0.81 (0.015)	0.598 (0.063)	0.789 (0.015)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running

The full model (herd size and distance to path) was selected as the best model in the models investigating ruminating ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 7.4$) and resting behaviours ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 20.1$; Table 3.8). Here, both behaviours share a positive relationship with herd size, and distance to path incurs a positive effect on resting behaviour and a negative effect on ruminating behaviours (Figure 3.19). Distance to the path was never retained as a sole significant predictor regardless of the behaviour modelled.($\Delta AIC_{distance} = >6$ for all behaviours; Table 3.8).

With regards to the PATH2 analysis, both herd size and distance to the nearest path were not retained as significant predictors in the models investigating the probability of alert, head-raised or locomotion behaviours exhibited by observed herds ($\Delta AIC_{null} = 0$ for all behaviours). Herd size was retained as the sole significant predictor in the model investigating ruminating behaviours ($\Delta AIC_{herd} = 0$, $\Delta AIC_{null} = 11.5$). Specifically, the probability of ruminating being observed increases with increasing herd size. The full model was selected as the best model in the models investigating foraging behaviour ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 31.4$), resting behaviour ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 39.4$) and active behaviours ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 39.2$). Specifically, distance to the nearest path was negatively

associated with the probability of observing resting behaviour, whilst a positive relationship was found with foraging and active behaviours, and herd size incurred a positive effect upon both foraging and active behaviours, and was negatively associtated with resting behaviours. Distance to the path was never retained as a sole significant predictor regardless of the behaviour modelled ($\Delta AIC_{distance}$ >6 for all behaviours).

Table A3.3. Summary of all beta-binomial retained models within 6 ΔAIC, ignoring more complicated model counterparts with higher ΔAIC (Richards, 2008). Outputs show herd behaviour analyses predicting the proportion of the herd engaging in behaviours whilst considering herd size (*HS*) and distances to all paths (*PD*) in the HA (PATH1), to paved-paths in the HA (PATH2) and to all paths in the IB. The degrees of freedom are denoted by '*K'*. Estimated coefficients for beta-binomial distribution parameter ϕ are detailed. '*K*' is the estimated number of model parameters and '*LL*' is the maximum log-likelihood.

Model	*Intercept*	*PD*	*HS*	ϕ	*K*	*LL*	*AICc*	Δ*AIC*
PATH1 HA								
PSF	0.708	-0.002	-0.07	0.999	4	-895.981	1799.961	0
PSR	-3.295	0.002	-0.061	0.257	4	-409.272	826.543	0
PRT	-1.689	0.002	0.095	0.999	4	-774.124	1556.248	0
PA	1.679	-0.002	-0.094	0.999	4	-776.724	1561.448	0
PL	-2.331	-	-0.0570	0.336	3	-376.567	759.134	0
PATH2 HA								
PSF	-2.478	0.001	0.148	0.999	4	-478.884	965.768	0
PSR	-3.949	-	0.132	0.223	3	-177.504	361.007	0
PR	2.250	-0.002	-0.187	0.999	4	-510.543	1029.086	0
PA	-2.243	0.002	0.187	0.999	4	-510.597	1029.194	0
IB								
PR	-1.815	-0.002	0.056	0.999	4	-616.835	1241.670	0
PA	1.700	-	-0.060	0.999	3	-617.507	1241.015	0

† PSF, PSR, PR, PA, PL represent proportion of herd engaged in foraging, ruminating, resting, active and locomotion behaviours. PD and HS represent distance to the path and herd size, respectfully. A '-' denotes the absence of a given variable in the best model.

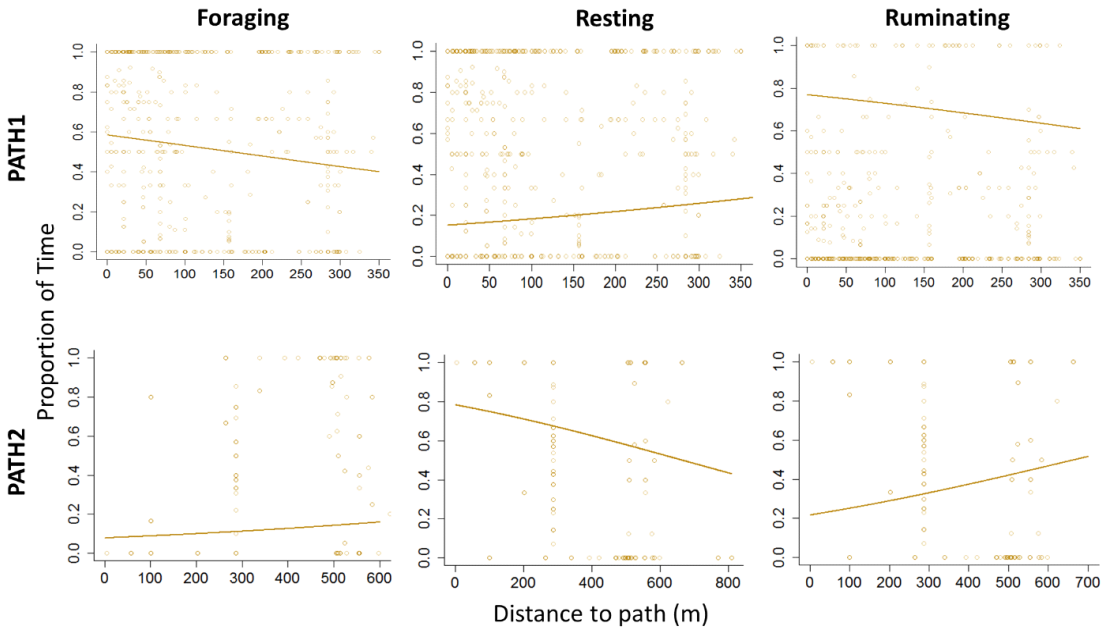

Figure A3.4. Proportion of herds exhibiting different response behaviours recorded in relation to distance to the nearest path in the HA. The best models generated from PATH1 data and PATH2 data are shown in the top row and bottom row, respectively. Data points have been jittered to show overlapping data. Here, results are generated from the full model, and the solid line indicates the best-fit model of the effect of herd size, calculated whilst holding herd size at the mean.

In the IB, no parameters were retained in the models investigating the probability of foraging, ruminating, head-raised, or walking behaviours exhibited by observed herds ($\Delta AIC_{null} = 0$ for all models listed; Table 3.7). Herd size was retained as the sole significant predictor in the models investigating active behaviours ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 6.5$), whereby the probability of observing active behaviours decreased with increasing herd size (Figure 3.20). The full model (herd size and distance to path) was selected as the best model in the models investigating resting behaviour ($\Delta AIC_{herd+distance} = 0$, $\Delta AIC_{null} = 7.4$), with the proportion resting increasing as herd size and distance to the nearest path increase (Figure 3.20). Distance to the path was never retained as a sole significant predictor regardless of the behaviour modelled($\Delta AIC_{distance} = >6$ for all behaviours; Table 3.8).

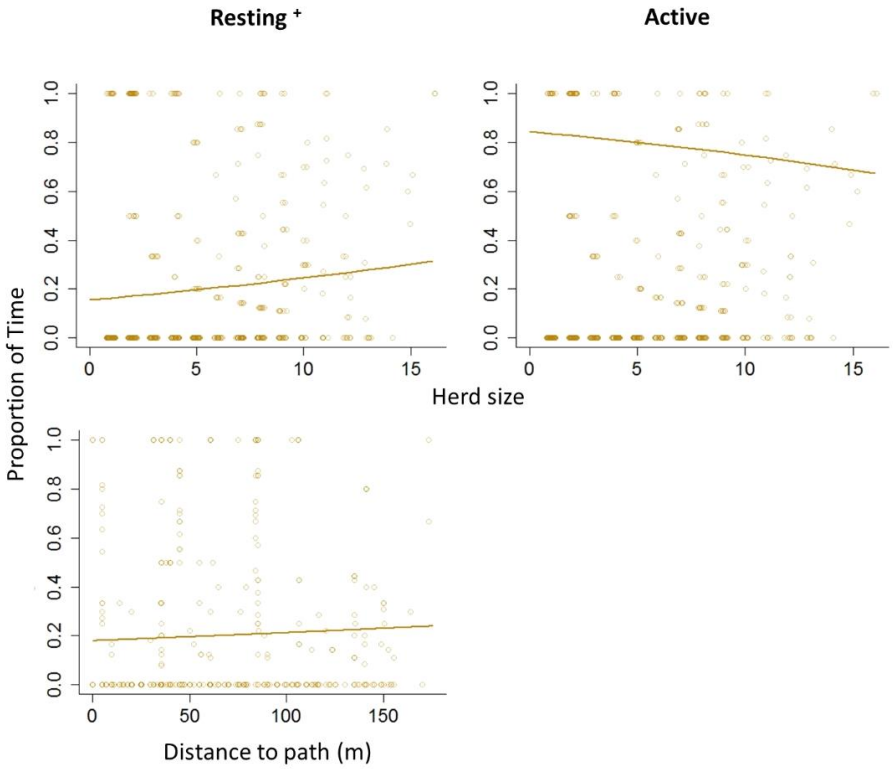

Figure A3.5. Proportion of herds exhibiting different response behaviours recorded in relation to herd size (top row) and distance to the nearest path (bottom row) in the IB. Data points are jittered. Solid line indicates the best-fit model of the effect of the predictor of interest (shown on the x-axis), calculated whilst holding the other variable at the mean when included in the best model (denoted by a '+').

Table A3.4. Proportion of red deer herds engaged in different behaviours whilst positioned on the following habitat categories: bracken (BR); bracken-grass (BRG); grass (G); bog (B); grass-heather (GH); heather (H) and heather-grass-moss (HMG). Figures listed are the mean proportions observed in a given behaviour (±SE) averaged across the total number of scans (N) respective to the appropriate habitat category. Running was never recorded in a scan.

Behaviour	BR (N= 24)	BRG (N=23)	G (N= 294)	B (N=53)	GH (N=26)	H (N=159)	HMG (N=28)
Foraging	0.562 (0.097)	0.576 (0.086)	0.618 (0.024)	0.294 (0.054)	0.466 (0.073)	0.404 (0.032)	0.612 (0.085)
Rest	0.354 (0.097)	0.152 (0.067)	0.247 (0.023)	0.539 (0.058)	0.294 (0.072)	0.392 (0.033)	0.072 (0.038)
Walking	0.073 (0.046)	0.115 (0.06)	0.072 (0.011)	0.038 (0.02)	0.119 (0.051)	0.07 (0.016)	0.057 (0.038)
Ruminating	0 (0)	0.105 (0.035)	0.058 (0.01)	0.117 (0.029)	0.112 (0.043)	0.098 (0.019)	0.183 (0.067)
Alert	0 (0)	0.073 (0.029)	0.02 (0.005)	0.012 (0.01)	0.112 (0.043)	0.05 (0.016)	0.109 (0.052)
Head up [a]	0.073 (0.046)	0.293 (0.076)	0.149 (0.017)	0.167 (0.04)	0.342 (0.092)	0.219 (0.03)	0.349 (0.086)
Active [b]	0.635 (0.096)	0.869 (0.081)	0.767 (0.024)	0.461 (0.058)	0.808 (0.096)	0.623 (0.035)	0.961 (0.041)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running; [c]

Removing unsurfaced paths from the analysis revealed herd size effects on foraging, resting and overall activity to contrast with those found under the PATH1 analysis, whilst ruminating patterns remained the same regardless (Figure A3.5). It is unclear as to why removing unsurfaced paths would cause a reversal in the relationship between the size of a herd with the proportion engaged in a given behaviour, especially in the case of resting, whereby herd size was the sole predictor in both PATH1 and PATH2 models. Given the anomalous nature of these results and considering that herd size was not a predictor of interest in this study, inferences were not made on the herd size effects on the proportion of herds engaged in a given behaviour.

During the day period, herds were mostly engaged in foraging behaviours for both the HA and the IB (mean proportional times = 0.552±0.021 and 0.659±0.026, respectively), whilst vigilance accounted for the

least displayed behaviour in both the HA and the IB (mean proportional times = 0.042±0.008 and 0.043±0.011, respectively). During the night period, herds were observed to be mostly engaged in foraging behaviours during for both the HA and the IB (mean proportional times = 0.479±0.03 and 0.583±0.02, respectively), whilst vigilance accounted for the least displayed behaviour in both the HA and the IB (mean proportional times = 0.025±0.008 and 0.033±0.007, respectively).

Table A3.5. Proportion of red deer herds engaged in different behaviours for both HA and IB sites calculated during the day period (HAD, IBD) and the twilight period (HAN, IBN). Figures listed are the mean proportions observed in a given behaviour (±SE) averaged across the total number of scans (N) respective to the appropriate site and light period combination. Running was never recorded in a scan.

Behaviour	HAD (N=407)	HAN (N=207)	IBD (N=207)	IBN (N=336)
Foraging	0.552 (0.021)	0.479 (0.03)	0.659 (0.026)	0.583 (0.02)
Rest	0.271 (0.019)	0.364 (0.031)	0.158 (0.021)	0.246 (0.02)
Walking	0.069 (0.01)	0.073 (0.014)	0.049 (0.011)	0.062 (0.009)
Ruminating	0.088 (0.01)	0.064 (0.014)	0.093 (0.015)	0.075 (0.01)
Alert	0.042 (0.008)	0.025 (0.008)	0.043 (0.011)	0.033 (0.007)
Head up [a]	0.2 (0.017)	0.162 (0.022)	0.185 (0.021)	0.171 (0.014)
Active [b]	0.752 (0.02)	0.641 (0.031)	0.845 (0.021)	0.754 (0.02)

[a] Head-up = Walking + Ruminating + Alert + Running; [b] Active = Foraging + Walking + Ruminating + Alert + Running